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The anatomy of the middle and lower pleistocene hominid femora.

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THE ANATOMY of the AHO MIDDLE ~~AND~~ LOWER PLEISTOCENE HOMINID ~~FEMORA~~ FEMUR

by

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Thesis submitted for the degree of
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BIBL LOND N DN

I.1: ABSTRACT: Although the femur is the most commonly preserved post-cranial bone of the fossil Hominidae it has seldom been the subject of detailed comparative investigations and has never been comprehensively investigated using the range of analytic and computational techniques now available. Moreover, recently discovered fossil hominid femora from east Africa have considerably increased the study sample, which has also included material from China, Java and South Africa. The basic comparative sample was formed from 100 Romano-British femora. In addition, a small number of modern Bushmen and several fossil femora of Upper Pleistocene age were included; femora from *Pan*, *Gorilla* and *Pongo* completed the comparative sample.

The femora included in this study have been investigated through a variety of analytic and statistical methods. A number of earlier workers have suggested that certain non-metric features of the fossil hominid femur differed either in their incidence or development from modern *Homo sapiens*. Such suppositions needed to be tested against a large comparative sample and an investigation of five non-metric traits formed one part of this study. Second, the bones were measured externally, using some techniques of earlier workers,

but including a number of new parameters formulated for this study. The most revealing information in this study was derived from the third part of the analysis. Radiographs were made on all femora included in this study and the metric evaluation of the radiographs has provided the clearest evidence of the alterations in the hominid femur through the Pleistocene.

The features and morphological complexes revealed in these investigations have been analyzed anatomically and biometrically and evaluated through univariate and multivariate statistical techniques.

The changes recognized in the internal and external examination of the femora are clearly of biomechanical significance and delineate an integrated total morphological pattern of the femur of the fossil Hominidae at at least two grades of organization.

I.2: ACKNOWLEDGEMENTS: A study such as this inevitably requires assistance and advice from many quarters. First, I would like to acknowledge, with great gratitude, the help of my supervisor, Professor M.H. Day. It was his work with the Olduvai Hominid 28 material which stimulated my own interest in the femur and eventually led to this work. During this study he has unfailingly and patiently been a source of advice and assistance.

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I.7: *INTRODUCTION:* Analysis of the locomotor behaviour of the early hominids is a field of study which could reveal important information regarding the development and diversification of the Hominidae. Although a number of fossil hominid femora have long been known from sites in China, Java and Africa field work in the East Rudolf area of Kenya in the last few years has significantly increased the amount of femoral material available for study. This thesis reports on an investigation of most of the known fossil hominid femora from Lower and Middle Pleistocene sites.

The femur is the most commonly preserved bone of the post cranial skeleton of the fossil Hominidae but studies on this bone have, in the past, largely centered on the more superficial aspects of the bone's morphology. Moreover, previous studies have been typological in orientation and the wider scope of population variability has not played a part in these analyses. The present study has employed several analytical techniques not extensively used in previous studies. Although a number of earlier workers have included radiographs in their studies of fossil femora these radiographs have never been analyzed in comparison with a large control population. Therefore, the

internal morphology of the fossil sample has never been brought into focus against the variability expected in a reasonably large and accurately sexed control group. Moreover, although multivariate statistics have demonstrated their analytical value in certain problems involving the skull and its components these techniques have not yet been applied to a large sample of fossil hominid femora. The present study has analyzed the fossil sample in comparison with several control groups utilizing a variety of univariate, bivariate and multivariate statistical techniques. The patterns of differences revealed by the anatomic, radiographic, biometrical and statistical investigations have been related to possible biomechanical models of the lower limb.

Section II of this thesis consists of a survey of the literature dealing with the hominid femur. After a review of the general literature a discussion of the many osteometric techniques which have been applied to the femur is given. This section ends with a review of the literature concerning each of the major sites or areas which have yielded hominid femora of Lower or Middle Pleistocene age. The East Rudolf specimens are not dealt with separately in this section since the literature on this material is not yet extensive.

Section III describes the methods and materials used in this study. Following a discussion of the osteometric, radiographic and analytical methods used here the comparative and fossil materials are described; the conditions of discovery, the state of preservation and the suggested age of the fossil sample are given.

Section IV consists of a combined presentation of the study results and a discussion of the significance of these results with regard to the individual specimens. Because of the large number of specimens included in this study it was thought expedient and convenient to combine the discussion of the results with the report of those results. The first part of this section deals with the analysis of the non-metric variables and the significance of these results, in statistical and anatomical terms, is discussed. The second part of this section consists of the radiographic and biometric analyses; the control groups are reported and discussed first followed by a discussion of each of the fossil specimens. The report of the multivariate analyses, given in the final part of this section, discussed the validity and significance of this data for the taxonomic position and attribution of the various fossil specimens.

After a concise presentation of the findings in Section V a review of the theoretical basis of palaeotaxonomic theory is given. It is pointed out that neontological systematics are structured around stringent, but demonstrable, criteria not available in palaeontological systematics. Moreover, a number of ontogenetic and phylogenetic factors may possibly distort the classificatory significance of certain features found on fragmented and fragmentary fossil material.

REVIEW OF THE LITERATURE

II.1: General Literature: Although anatomical interest in the femur has a considerable history, anthropological interest was first stimulated by the discovery of the Neandertal skeletal material in 1856. In the absence of established anthropometric techniques the first report on the Neandertal material (Schaffhausen, 1858) contained only four measurements on the femur. It was apparently the discovery of the Les Eyzies material which prompted Broca (1868) to propose standardized anthropometric techniques and procedures. Although Broca had earlier (1867) published some scanty data on the intermembral indices of a small sample of Europeans and Negroes, his report on the Les Eyzies fossil hominids (1868) must stand as the first true anthropometric study. In this study, he gave length, anteroposterior and transverse midshaft diameters of the femora and estimated the total living height of each individual from the length of the respective femora using "tables par les medicines legistes".

Wolff (1870, 1892) who extrapolated and developed ideas proposed earlier by Culmann (in von Meyer, 1867) and von Meyer (1867) proposed a theoretical explanation of bone structure. "Wolff's Law" (1892) stated that "Every change in the form and function of a bone or of a function alone, is followed by certain definite changes in the internal

architecture and equally definite secondary alterations in the external conformation in accordance with mathematical laws" (translation quoted from Townsley, 1948). The trajectorial theory arose from this description of how form follows function in bone in order to explain long-bone stress patterns. The theory, according to Wolff, was that the trabecular density patterns in cancellous tissue followed the lines of maximal internal stress. The basis of Wolff's explanation of the orientation and density of trabecular bone is based on the "orthogonality" of the total pattern; that is, the lamellar structures reportedly cross each other at right angles. According to engineering principles, the most efficient resolution of stress is achieved through right angle structures.

Implicit in Wolff's theory is the concept that tension results in osteoblastic activity. Although this has been supported by some workers (Roux, 1883; Townsley, 1948; Scott, 1957) others have suggested that tension results in osteoclasis (Volkmann, 1862). Hoyte and Enlow (1966) have suggested a compromise in that both processes may occur: "Within the attachment area of a single muscle both resportion and deposition may occur simultaneously". They also pointed out that the actual cause and effect mechanisms of bone dynamics are not known. Wolff's theories have also been criticised on engineering principles. Perhaps the main

criticism is that bone is a non-homogeneous material and as such should not be structurally analyzed in the same way as single phase building materials. Moreover, as Evans (1953) has pointed out, engineering formulae are constructed to deal with tension in only two dimensions while bone must deal with three dimensional stresses; Williams and Svensson (1968) have recently shown, however, how stresses in three dimensions may be analyzed.

Kuhff (1875) used diverse material (from Dolmens in Lozere, n=5; "Carlovingians", n=4; "Gallo-Romans", n=6; and Neolithic from Baye, France, n=6) in publishing a study on the morphology of "prehistoric" femora. This was the first time that the bowing and the torsion of the human femur had been measured. His method of measuring bowing of the femoral shaft (see Section II, 2, ii) was later criticised by Manouvrier (1893) who pointed out that Kuhff's method was really measuring two unrelated features - the curvature of the shaft and the size of the epiphyses. Kuhff concluded that the "prehistoric" femur showed a high degree of torsion more frequently than did the modern femur and that this torsion is often associated with the curvature of the shaft; the size and composition of his sample, however, does not seem adequate to support such a conclusion. He proposed an "indice angulaire" and suggested that it was an important feature in determining the sex

of the femur; the "indice angulaire" was defined as the mean between the angle of shaft obliquity and the angle of the neck with the shaft - males were said to average about 8° and females about 14°.

The first study by an American on the human femur (Gillman, 1877) discussed anteroposterior flattening of the proximal and distal ends and stated that the flattening of the femur "in every case" was associated with transverse flattening of the tibia. He also stated that the "cortical substance is uncommonly thickened" in the flattened bones; however he gave no measurements to support his observations. The sample of 21 Amerindian femora was derived from tumuli at Great Mound, Michigan.

Mikulicz (1878) examined 120 "Viennese" skeletons and found 10 femora in this sample that showed negative torsion of the femoral head; in this group of mixed sexes he showed a range of the torsional angle of the neck with the shaft of -25° to +37°. This range is larger than that reported by any other worker.

Garson (1879) investigated the effect of side on 70 pairs of femora and tibiae. From this study he concluded that:

28.6% of the right femora were longer than the left
58.5% of the left femora were longer than the right
12.9% of the femora were equal in length.

These results were criticized by Pearson and Bell (1919) who, in a much more comprehensive investigation on the effect of side on femoral parameters, were unable to find any significant difference. Garson's work may be further criticized on the basis that this was a mixed sample and he made no attempt to discriminate between sex, age or race.

The major sea voyages of the last few decades of the 19th century produced a number of monographs on hitherto unstudied aboriginal peoples. These studies were, without exception, typological in nature and utilized very small samples. Flower (1879, 1884) reported on the natives of the Andaman Islands. In the earlier work, using a sample of 19 skeletons, he reported only the length measurements on the femur and estimated the total living height using Humphrey's formula (see Section II. 2. i). In the later paper, his sample was extended to 29 skeletons and he reported, in addition to the length measurements, femoro-humeral and femoro-tibial indices.

Although Waldeyer (1880) had noted the occurrence of the third trochanter[1] and fossa hypotrochanterica in primates and man, Houzé (1883) was the first to discuss the importance and frequency of these features in man. The term "fossa hypotrochanterica" was proposed by him at that time to describe a groove in the area of the insertion of the gluteus maximus muscle. Using a sample of 110 Neolithic and 67 "Modern Belgians" Houzé concluded that both the third trochanter and the fossa hypotrochanterica were more common in primitive man than in modern man and gave percentage values, based on his sample, to support his view. Furthermore, he divided the human races into "megapygous" and "micropygous" groups and termed the anthropoids "platypygous" on the basis of the development of the gluteus maximus muscle. He also pointed out the difficulty of sexing fossil femora; the two features under discussion, he stated, are sometimes more developed in females than in males and the third trochanter may appear more often in females. These observations have found support by later workers (Pearson and Bell, 1919; Hrdlicka, 1938) although in the present study, females showed a slightly lower percentage of the occurrence of the third trochanter (43.4%) than did the males (56.6%) (See Table VII)

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[1] The term "third trochanter" was first used in the Second Edition of Cuvier's Leçons d'Anatomie Comparee, published in 1835. The term "apophyse en forme de crochet", apparently referring to the same feature, appeared in the 1805 edition of the same book.

Occurrence of Third Trochanter

Group	Number	Percentage
Negro	16	12
Polished Stone Age	110	38
Modern Brussels	67	30.15

Occurrence of Fossa Hypotrochanterica

Negro	16	6
Age of Reindeer in Belgium	?	60
Quaternery Epoch	44	"very frequent"
Polished Stone Age	110	20
Modern Brussels	67	10

Simultaneous occurrence of both features

Polished Stone Age	110	24[1]
Modern Brussels	67	5
Negro	16	6

(Houzé 1883)

Garson (1883) after the examination of a single, possibly female, skeleton discussed the "Osteology of the Ancient Inhabitants of the Orkney Islands"; the analysis of the femora gave only the maximum length measurement.

Owen (1884), coining the (undefined) term "Anthropotomy"

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[1] This figure is clearly impossible since only 20% had the fossa.

described the two Tilbury femora; he gave only length (16½ inches) and circumference (3 inches, 9 lines[1]). He discussed a "considerable tubercle on the anterior surface at the median extent of the intertrochanteric line". Re-examination of the original material did not, however, disclose any "anomaly" at this position. The bone does show probable evidence of rickets which Owen failed to mention. The "marked third trochanter" pointed out as "noteworthy" is of very slight development in comparison with a large sample. He also suggested that the shaft was "thicker and stronger" than in modern man but he provided no measurements nor comparative data to support such a statement.

Thomson and Murray (1884) on the HMS Challenger during its visits to many Pacific Islands, examined the skeletal remains of a number of groups. The femoral data they published gave only length measurements.

Turner (1886) examined seven Maori femora and described, for the first time, the infra-trochanteric ridge. This feature he ascribed to pronounced development of the gluteus maximus muscle because of squatting.

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[1] A "line" is equivalent to 1/12 of an inch (National Encyclopaedia, 1881)

In the following year, Turner again discussed the effects of squatting on the femur. He suggested that a prominent linea aspera and platymeria were found more frequently in people who habitually squatted or stooped. This occurred because the gluteus maximus muscle "is made tense ... and pulls more or less continuously" on the upper part of the femur.

In a very fine descriptive paper, Fraipont and Lohest (1886) discussed the major characteristics of the Spy femora. They pointed out that the three femora (a right from Spy I and a right and left from Spy II) were very similar in most respects to the Neandertal material from Germany. Specimens from both sites, they stated, were characterised by robusticity, thickness, marked curvature and torsion of the shaft and by the great volume of the head and condyles. This last feature, the considerable development of the distal articular surface, they suggested is not present among modern races with the possible exception of the "indigenes des Phillipines". They concluded that because of the pronounced backward extension of the condyles, fully erect posture was not possible. Humphrey (1888) described anatomic and ontogenetic factors which might affect the angle of the femoral neck. He stated that the neck angle is smaller in longer bones than in shorter bones and is usually smaller when the pelvis is wide. He also suggested that although there is considerable variability in the neck angle within a

population, the angle does not change once growth has been achieved, as long as normal function is maintained; bed-ridden individuals may however develop a wider angle. This view has been challenged by Brooks and Wardle (1962).

Manouvrier (1889) examined a Neolithic burial at Crecy-en-Brie and proposed the term "platymerie" and constructed the "indice de platymerie" to indicate the degree of proximal anteroposterior flattening shown by these femora. He suggested that this flattening, as well as platycnaemia of the tibia, was due to mechanical stress on the leg during locomotion. Manouvrier suggested that "la marche ascendente sur les terrains raboteux ou accidentes" would affect the lower limb in several ways:

1) retroversion of the tibial head
2) accentuation of the curvature of the femur
3) enlarged linea aspera
4) presence of a third trochanter and fossa hypotrochanterica
5) platymeria

The platymeria would be due, therefore, to hypertrophy of the proximal portions of the crural muscles because of the increased stress on the knee joint while climbing over rough ground. Hepburn (1897b) accepted this explanation and added that extension of the knee must be associated with extension of the hip; this, he stated, would be reflected in an enlarged gluteal ridge and the formation of a third trochanter.

In an attempt to refute the views of Wolff (1870), Dwight (1890) attempted to show that the third trochanter and a process for the teres major muscle on the scapula "cannot, in many cases at least, be accounted for by a mechanical explanation, and further that it can hardly be doubted that useless and rudimentary structures occur in bones". Documentation for this view was based on a sample of 79[1] Amerindian femora:

True third trochanter on both sides	7
True third trochanter on one side	3
Rough ridge ... on both sides	16
Rough ridge ... on one side	2
No true third trochanter	48
No true third trochanter on one side; doubtful on the other	3
	79

Dwight stated that 3 individuals which showed a true third trochanter on one side were "sub-adults" and one which showed this feature on both sides was a "girl of thirteen". Dwight did not disclose how he was able to ascertain the age of this individual so precisely. He concluded that the occurrence of this feature in small females and sub-adults rules out muscular development as

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[1] Dwight stated that his sample comprised 67 bones but his data shows that sum to be wrong.

a cause; equally "in some cases at least an appeal to heredity is absurd ... even if we cannot fully explain it".

Bertaux (1891) argued against a biomechanical origin for the formation of a pilaster in the human femur. He reasoned that since the anthropoids had similar muscles, but without the development of the linea aspera, then the source of this feature must be sought elsewhere. He therefore suggested that pilaster formation in man is a racial or "ethnique" feature.

Scott (1893) investigated skeletal remains from New Zealand and the Chatham Islands but his report on the associated femora gave only upper and mid-shaft diameters and four length measurements.

Manouvrier (1893) attempted to show that certain features of the lower limb widely thought to be primitive, "atavistic" characters (i.e. platymeria and femoral bowing, platycnaemia and retroversion of the tibial head) were instead due to "de modifier dans sa forme le travail des membres inferieurs". He again argued in this paper, as he had done in 1889, for a mechanical origin of the above-mentioned features; platymeria and pilaster formation were said to be due to "agrandissement du muscle crural". These two features were thus closely related and the maximum thickness of the pilaster was said to occur at the level

of maximum bowing. He further observed that robust femora often show the greatest development of the pilaster and bowing and that these features are seldom seen in infants and females. He provided the following data to support this argument:

Group	Degree of Flattening	Pilastric Index
19 femurs	Platymery "accentuée"	100.5
18 femurs	Platymery "faible"	104.0
17 femurs	Platymery "nulle"	110.3

(Manouvrier 1893/132)

Manouvrier also suggested that the mechanical axis of the femur (from the centre of the femoral head to the "centre of the condyles") is situated behind the anatomical axis of the bone. Because of this difference in axial orientations the bowing and consequently the pilaster are formed "pour resister au poids du corps".

Matiegka (1893), like Garson, investigated the effect of side on the length of the femur but unlike that author correlated his data with age. Thus correlating maximum femoral length with age groups:

	Number	L=R	L>R	L<R
Adult male	13	2	11	0
Adult female	12	5	3	4
Males, 12-21 years	24	7	12	5
Females, 9-19 years	4	2	1	1

Thus while Garson found 12.9% of his larger sample to be equal in length Matiegeka found 13.9% equal in length; however the remainder of his results are comparable neither with Garson nor with Pearson and Bell (1919) undoubtedly due, in part, to the small size of his categories.

Charles (1894) examined the effects of squatting and sartorial positions on the lower limb of the Punjabi. He did not disclose the number of femora examined but he had a sample of 52 tibiae. He concluded that extra facets would be produced on the femur, tibia and astragalus as a result of habitual use of these positions. Moreover the cotyloid notch in the acetabulum "in every well-marked Punjabi pelvis" is partially enclosed by bone; this enclosure is primarily ligamentous in the European pelvis. With specific regard to the femur, a number of responsive features were said to occur. The articular surface of both the head and internal condyle would be increased by means of extensions of the articular surface.

The extension of the femoral head onto the supero-anterior surface of the neck was named "Poirier's facet" by Evangeli-Tramond (1894) after the first anatomist to note its occurrence.

The Poirier's facet was said, to develop in response to changes in the acetabulum that occurred under the stress of extreme flexion and partial abduction during squatting.

Lehmann-Nitsche (1895) examined a number of femora from row graves at various sites in central Europe. He included platymeric, pilastric and robusticity indices and estimates of living stature. From his data he concluded that flattening of the upper femoral shaft is often associated with a high pilastric index, a correlation previously noted by Manouvrier (1893). Thus:

Site	No.	Platymeric Index	No.	Pilastric Index
Row graves in Germany	87	79.7	94	105.3
Row graves in Bajuvar	30	80.2	182	103.8

(Lehmann-Nitsche, 1895)

Newton (1895) in describing the two Galley Hill femora, gave two differing lengths (419 mm and 421 mm) for the same specimen. He measured the mid-shaft diameters and stipulated that the linea aspera should be avoided in the anteroposterior orientation (difficult if not impossible in that position). He stated that the shaft was "nearly straight" although Pearson and Bell (1919) obtained a Primary Index of Bowing of 2.7 for this specimen. Newton gave various other measurements of the head, neck and condyles but unfortunately failed to record his techniques.

Hepburn (1897b) dealt mainly with the three major shaft indices, head diameter and length, using a very heterogeneous sample of 142 *Homo sapiens* and 10 anthropoids. He felt that the selected parameters would indicate the "sum-total of those diverse modes of life in relation to the attitude and gait of the individual which characterize different races of mankind ... (which) would enable one to determine with considerable precision the race to which a particular group of bones belongs ...". His results, however, do not support this optimistic goal; moreover parts of his sample do not correspond to any recognized racial grouping. For example, such groups as "Hindoo", "Sikh", "Bengalee" and "near an old Roman wall at Leicester", could hardly, using any criteria, be considered racial! In examining his results on the Platymeric Index, for instance, we find that while the lowest index (58.8) occurred in a Maori and the highest (115.0) in a British femur, a value of 60.0 was also found in the British sample. Again, while the average index for the Eskimo (n=4) was 88.3 the average for the Gibbon (n=2) was 87.4. The remainder of his observations indicated the same sort of overlap and wide intra-group population ranges so that the indices were of little, if any discriminatory value.

Warren (1897) examined the variability in skeletal

material recovered by Flinders Petrie near Thebes in Egypt. This material, named the "New Race" was between 3000 and 4000 years old. His measurements included maximum and oblique length, angle or torsion and the length of the head and neck; he also gave Pilastric Indices for 5 specimens. For these measurements, dealing with a sample size of between 80 and 113, he calculated the mean, the standard deviation and the coefficient of variation. He concluded (contrary to the findings of Garson, 1897) that there was no difference in the variability of the two sides. The length of the head and neck was said to be important for sexual discrimination: male $\bar{m}$ = 158.6 mm; female $\bar{m}$ = 154.0 mm and he further suggested that the degree of shaft torsion would be important as a racial character. His figures for shaft torsion are:

Male range : +2° to +39°; s.d. = 8.0° (n=33)

Female range : +9° to +42°; s.d. = 7.7° (n=80)

He did not, however, provide the comparative data necessary to support this contention. The sex of the specimens, which were all associated skeletons, was ascertained by "general appreciation" of body morphology plus examination of the mummy wrappings which often gave information as to sex.

Bümuller (1899) gave a wide range of femoral measurements for a sample of 404 modern Bavarians, 5 "greater anthropoids"

1 gibbon and 4 "monkies". This paper included the use of mathematical correlations between femoral features, in this case between the Pilastric and Platymeric indices. His method of demonstrating degrees of correlation involved plotting categories of measurements rather than individual measurements. He stated that the Pilastric Index reached a maximum value in childhood and decreased thereafter; conversely the Platymeric Indices and Popliteal Indices were said to be low in children and to show increase with age. In this paper, Bumuller proposed that the *"Pithecanthropus"* I femur belonged to a new species of gibbon, *Hylobates giganteus*. This suggestion was made primarily because of the similarity of the values of the Pilastric and Popliteal Indices between *"Pithecanthropus"* I and living gibbons.

PILASTRIC INDICES

Platymeric Indices	-90	90-100	100-110	+110	Under 100 + Pilaster	Totals
+100	0	1	22	24	1	48
99.9-85.0	11	15	62	33	8	129
84.9-80.0	12	14	30	9	8	73
-80	28	26	47	9	44	154
TOTALS	51	56	161	75	61	404

It is difficult to evaluate these results very precisely.

H is categories are large and the boundaries between the Pilastric Indices are not clear; for example, to which group would a Pilastric Index of 100 or 110 belong? Moreover, this table contradicts the suggestion by others (Manouvrier, 1893; Lehmann-Nitsche, 1895) that low Platymeric Indices are found more often with high Pilastric Indices. It was however confirmed by Pearson and Bell (1919) who found a correlation of +.510 between these indices. It is probably valid to assume that the small sample sizes used by Manouvrier and Lehmann-Nitsche biassed their results.

Walkhoff (1904) was the first to use x-rays in the study of fossil human femora. In his study of the Neandertal and Spy material he provided radiographs of the proximal and distal portions of the femora. He suggested that the femora displayed three "systems" of trajectorial lamellae; System I or the "static trajectorium" was said to occur only in species where erect posture was habitual. Gieseler later (1925) objected to this definition since he stated that he could detect System I in some anthropoids.

Dwight (1905) attempted to define certain features of the long bones which might be useful in sexual discrimination. Using a sample of 100 males and 100 females from the dissecting rooms of the Harvard University Medical School

he was forced to conclude that although there were considerable differences between certain features, perhaps as many as 75% of the specimens could not be reliably sexed on osteometric data alone. The most reliable parameter, however, he felt was the maximum diameter of the head, thus:

$\bar{m}$ maximum head diameter	male =	49.68 mm
	female =	43.84 mm
$\bar{m}$ difference		5.84 mm

However, by using the ranges of this parameter instead of the means he found 113 (28.9%) which overlapped with the range of the opposite sex; this overlapping was restricted to a range of 3 mm (from 46 to 48 mm).

Guldberg (1905) attempted to show a relationship between bowing of the femur and the age of the individual. He discussed a flat or straight femur as being "infantile" the adult maximum of bowing would be reached between 8 and 12 years of age. *"Pithecanthropus"* I fell into the "infantile category".

Gorjanovic-Kramberger (1906) described the two left femora from Krapina: I from an adult and II from a "younger" individual. In his study, he compared radiographs of these specimens with those taken by Walkhoff (1904) of the Neandertal and Spy femora. Both Krapina specimens reportedly show sealed epiphyseal

lines and demonstrate the presence of Ward's Triangle. He concluded that the Krapina specimens showed close resemblance with those described by Walkhoff.

Discoveries of fossil human material began prior to 1872 in the four caves at Grimaldi. In 1872, an adult male was recovered from Barma del Caviglione; two fragmentary human bones had apparently been recovered earlier from this site. In 1873, three individuals were recovered from Baousso da Torre. Between 1884 and 1894, parts of six individuals were taken from the cave of Barma Grande and in 1874-5 five individuals were recovered from the Grotte des Enfants (Oakley et al. 1971). A possible total of 26 femora have therefore been excavated from the Grimaldi Caves[1].

Antony and Rivet (1907) dealt mainly with curvature of the femoral shaft; their sample included a

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1. The major reference for this material is R. Verneau, 1906 "Anthropologie, Monaco", volume 2. Although widely referred to as a journal (Bello y Rodriguez, 1908; Pearson and Bell, 1919; Boule and Vallois, 1957 and others) the work is actually a book in two volumes. I have unfortunately been unable to trace these volumes.

group of Pre-Columbian Indians (69 males, 52 females), 26 gorillas, 19 chimpanzees and 15 gibbons. In addition to proposing a new method of measuring femoral bowing (described in Section II.2.ii) they gave the major head and neck parametes and angles, some shaft data and the condylar measurements for this sample. Using a method of correlation similar to that of Bumuller", which plotted categories of Pilastric Indices against categories of radii of curvatures, they demonstrated that high pilastric indices were associated with the greatest radii of curvatures and vice versa. Their findings are:

Number	Pilastric Index	Radius of Curvature
20	118.3	96.3
19	111.5	110.4
14	105.0	126.1
11	115.6	106.0
12	108.0	110.9
14	103.2	118.3

This data would seem to confirm their contention that there is a positive relationship between the bowing of the shaft and Pilastric Indices; the results of the present study and their implication are discussed in Section IV. While rejecting a mechanical origin for femoral bowing they do not seem to offer a clear explanation either for its occurrence or for its

correlation with the Pilastric Index. They do state, following Manouvrier, that a "compensating effect" is present: the pilaster is formed by the extensive development of the crural muscles and in order to provide more area for this attachment the anterior face would be bowed outward.

Bello y Rodriguez (1908) examined a very mixed sample of 52 femora derived from "Cro-Magnon, ancient Gauls, Patagonians, Polynesians, Merovingians, Modern French and Germans". Although values for oblique length, upper and mid shaft diameters and indices were included in the paper, this was basically a study of non-metric variables. He suggested that the fossa hypotrochanterica and platymeria often occur together apparently to increase the surface area of the anterior aspect of the femur. He also described the existence in some femora of a "grand gouttiere" on the anterior face which extends distally from the intertrochanteric line. (This seems to be equivalent to the "crural trough" of Weidenreich and others). He demonstrated that this feature was developed to a remarkable degree in certain Patagonian and Peruvian specimens. He also pointed out that torsion and the Pilastric Index may be of little "valeur ethnique" because of the wide range of variability. He also

described the occurrence of supernumery tubercles including a "tubercle pretrochanterien"; although not figured, this would seem to be equivalent to the tuberculum hypotrochanterium described by Weidenreich as being characteristic of *"Sinanthropus"*.

Mollison (1908) measured a sample of 6 Maori and 2 Anau (ancient Persians) and provided data on shaft torsion, obliquity, bowing and the major shaft indices.

Turner (1909) described a single Tasmanian skeleton from Flinder's Island and made observations on curvature and muscle markings and provided the Platymeric Index. The Pilastric Index was said to be "below the European, (and) higher than in Neolithic and in the Maori femora" (ibid). However no figures were provided to support this statement.

Of the six individuals known from the Mousterian occupation site at La Ferrassie, in the Dordogne, only 1, an adult male, and II, an adult female, had associated femora which were complete enough for study. Although Ferrassie I was discovered in 1909 and Ferrassie II in 1910 (Oakley et al. 1971) the postcranial material has never been adequately described. Capitan and Peyrony (1909, 1910) published brief reports and stated that detailed reports were to follow.

As late as 1957, however, Piveteau could state that the Ferrassie material had not yet been "l'objet d'une ètude approfondie" (Piveteau, 1957/454).

Klaatsch (1910) using comparative data gathered for an earlier study on the femur (1900) published an analysis of the Spy and Neandertal skeletal material and concluded that man must have had a polyphyletic origin: "Primogenial Man", including the Neandertals, had a "gorilloid" ancestor, while modern man, first seen in "Aurignac Man" had a more gracile "orangoid" ancestor. There were said to be a number of differences in the femora of these two lines: the gorilloid line was generally more massive, had a higher Index of Robusticity and a larger head, and perhaps most importantly, the preservation of a cylindrical shaft section until just above the condyles. The "trumpet shape" or more gradual expansion of the distal shaft was said to be characteristic of the "orangoid" line leading to recent man.

Boule in his studies of the single individual from La Chapelle-aux-Saints (1911, 1912) provided a few measurements on the left femur; measurements on the right femur were not given since the differences between the two were "peine sensibles". He gave only a reconstructed maximum length, mid-shaft diameters and robusticity,

pilastric and popliteal indices. Boule concluded that the bones of this man had retained "l'empriente ou le souvenir d'un etat anterieur de grimpeur" and further that "La position accroupie habituelle des hommes fossiles et des peuples sauvages est aussi une survivance ancestrale" (1912/184).

The skeletal material from Paviland Cave was studied by Sollas in 1913. The major shaft diameters and indices were given as well as length on the left femur. He concluded that they represented the "Aurignacian" race.

Parson's studies on the English thigh bone (1913, 1914, 1915) dealt with a sample of 300 femora from a 13th and 14th century burial ground at Rothwell, Northants. His comparative sample (n=53) were dissecting room specimens from Guy's Hospital and St. Thomas' Hospital. The study included 9 parameters, the index of bowing, neck angle and torsion and one observation on the "presence of roughness of the front of the neck". The analysis of this material included sexual and side differences in the femur and comparison of the mean values for the various parameters in the Rothwell series with similar values in the modern group. Perhaps the most important fault with this work is the arbitrary nature of his sexual criteria. Extrapolating from the dissecting room material, of known sex, to the Rothwell series he formed 2 major tests of sex:

(1) Head diameter - male = +47 mm

female = -45 mm

(2) Breadth of condyles

male = +72 mm

female = -71 mm

Parsons later (1915) attempted to substantiate his sexual criteria by increasing his dissecting room sample to 82 femora. This study confirmed to him the value of head diameter as a sexual discriminator; he claimed a success rate of 91.5% by using this parameter alone. He also suggested, in this paper, that certain allowances should be made when comparing "wet" dissecting room material with dry bones; to account for drying, 1 to 3 mm. should be subtracted from wet bones to make their measurements comparable with dry specimens.

Lee (1914) published a paper in which she criticised Dwight's (1905) results on the basis that his small sample had produced an abnormally distributed Gaussian curve. It is apparent that she did not carefully read the paper she criticised. In order to test Dwight's results she took a sample of 279 femora and plotted the frequencies of head diameters. Two separate peaks appeared in a bimodal distribution, one at 49.83 mm and another at 43.72 mm. Her conclusion was that these peaks rather than Dwight's means, represent the means of the male and female specimens. Rather than cast discredit on Dwight's results, these figures stand as confirmation of his data. Firstly, he

had used a larger sample than Lee (400 femora of known sex); secondly, his two means were 49.68 and 43.84 mm. Nevertheless, Lee's method of frequency plotting bimodal Gaussian curves has interesting and largely untried possibilities in osteometric studies involving sexual discrimination.

Tamagnini and de Campos (1916) provided correlation coefficients for various femoral parameters in their osteometric study of the Portuguese; they were thus among the first to use statistics, in the modern sense, in the analysis of the femur. Their sample size exceeded 250 for certain parameters but most of their data was based on 134 male and 126 female femora. Unfortunately they did not record their raw data and some of their correlations have been questioned by later workers who obtained substantially different results (see especially Pearson and Bell, 1919). Their most significant correlation figures are:

	Male	Female
Length of bust[1] and distal articular width	.43±.05	.52±.04

[1] The "bust" in Tamagnini and De Campos' terms comprises the head and neck to the level of the inter-trochanteric ridge.

	Male	Female
Length of bust and diameter of head	.48 * .04	.51 * .04
Distal articular width and diameter of head	.63 * .03	.63 * .03
Collar angle[1] and shaft obliquity	-.06 * .06	-.13 * .06
Length of bust and obliquity	-.01 * .06	.04 * .06

Their correlations between the oblique femoral length and various parameters revealed no significant values although Pearson and Bell (1919) did report certain significant figures, especially between total length and the size of certain proximal and distal articular parameters.

Foote (1916) produced the first study on the comparative histology of the femur. In this study he examined 600 femoral mid-shaft cross sections of a wide variety of animals, including 139 humans. He defined three types of cortical bone:

1). Lamellar - a simple structure with 1, 2 or 3 concentric rings in uniform layers. This type occurs in amphibians, reptiles, bats and early foetal humans. The sheaths are separated from each other by vascular canals

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1. The collar angle is defined as the angle at which the central axis of the neck meets the central axis of the shaft.

which run parallel with the long axis by the shaft.

(2) Laminar - a variable number of concentric sheaths surrounding the medullary canal; the vascular canals may run tortuous courses. This type is found in birds, lower mammals, some amphibians, late foetal and early childhood humans.

(3) Haversian - comprised of cylindrical, concentric lamellar structures enclosing a Haversian canal; these canals may run tortuous courses; the linea aspera is always composed of Haversian bone. This type is found in reptiles, some birds and amphibians and man.

Foote formed a Medullary Index to demonstrate the relationships between the cortical and medullary diameters.

$$\left[\frac{(\frac{a+b}{2})^2 \times 100}{(\frac{A+B}{2})^2 - (\frac{a+b}{2})^2} \right] = R$$

where: a and b = long and short diameters of medullary cavity

A and B = long and short diameters of bone (i.e. cortex)

R = ratio of medullary cavity to bone.

Medullary Index

Amphibians		36.6	
Reptiles	(including turtle)	26.1	
	(excluding turtle)	33.0	
Birds		159.0	
Bats		48.0	
Human:	Black	41.9	n=34
	Yellow	43.8	n=23
	Ancient Egyptians	39.5	n=9
	Modern White	35.8	n=73
	$\bar{m}$ *Homo sapiens*	38.6	n=139

Understandably, perhaps, the hundreds of cross-sectional drawings reproduced in this paper are all reduced to the same scale; however, in the absence of any scale or size indication comparisons are difficult. Moreover, anatomical orientation is never given on the plates; nevertheless, this is the only paper which deals with the comparative histology of the femur and his findings are of interest, however suspect his plates.

Foote gave a long discussion of "senile" changes in the femoral cortical structure but he does not state how the age of this material was determined. It seems unlikely that the "age" of his specimens represents more than a guess. In senility, Foote stated, "the

lamellae around the Haversian canal becomes dark from a deposit of inorganic granules ... The granules increase as the process goes on, involving lamella after lamella, until the whole system is opaque and black. After the lamellae have reached this stage they are gradually broken down in amorphous particles which drop into the Haversian system and are removed by the blood vessels ... The inter-Haversian lamellae follow and a cavity is formed, which in the section appears as a space. This process continues".

John Koch, writing in 1917, reviewed the history of the biomechanical theories of bone structure and summarized the engineering and mathematical proofs on which the theories rested. He pointed out that Culmann's mathematical model, based on calculations for a solid body with a load on the head parallel with the long axis of the shaft, is not correct for a human femur, moreover, he stated, the model completely eliminated the greater trochanter from the calculations.

Koch estimated that the load on the femoral head during walking was 0.8 x body weight this figure has been challenged by Williams and Svenson (1968) who pointed out that he had ignored the dynamic effect of the muscles during locomotion their own work suggested

a load of 6 times body weight during static standing and walking. From his studies on bone architecture Koch concluded that:

> "the inner structure and outer form of the femur are governed by the conditions of maximum stress to which the bone is subjected normally by the preponderant load on the femur head" (1918, p. 273). Moreover, "the thickness and closeness of spacing of the trabeculae varies in proportion to the intensity of the stresses carried by them" (ibid. p.267).

Koch's descriptions of the trabecular systems were based on examination of longitudinal sections of the bone; these descriptions would seem to point out the fallacy of Garden's later (1961) analysis of the proximal femoral patterns as largely radiographic phenomena. The "trabecular" or "trajectorial" theory, as advanced by Koch and others, has been criticised on the basis that the discontinuous nature of the cancellous filaments are an inefficient method of dealing with weight bearing stresses in the femur. It is true, as Koch pointed out, that cancellous tissue is less efficient than compact tissue for dealing with longitudinal stresses. This criticism would seem, however, to ignore the complex biomechanical stresses in the femur and the basic mechanical function of cancellous tissue itself. Koch demonstrated mathematically that cancellous tissue reaches its greatest density where the vertical shearing forces and bending moments are greatest - i.e. in the proximal and distal portions of the bone. In other words, cancellous tissue does not function primarily as weight bearing tissue but acts rather to resist the lateral and bending stresses on the bone.

Holtby (1918) measured 56 male and 44 female dissecting room specimens in order to define, typologically, the "modern" English femur. He was not able to make such a definition and his main conclusion was that there seemed to be no correspondence between flattening at the proximal end and pilaster formation at the mid-portion of the femur. His reasoning followed the line that if platymeria is due solely to the muscular activity of the vasti (as suggested by Manouvrier and others) then their attachment area along the linea aspera should show development. Since he could not demonstrate a correlation between these features, Holtby concluded that these features must have different causes. He also stated that there was no relationship between bowing, pilaster formation and platymeria. He did not, however, provide mathematical correlations or any statistical evaluations to support his arguments.

The encyclopaedic four volume monograph by Pearson and Bell (1919) is the most ambitious and comprehensive work on the femur yet attempted. It is, moreover, the fullest demonstration of the biometrical-typological approach in the analysis of anthropometric data. The work represents an attempt to draw together, compare and correlate all of the work that had been done on the femur prior to 1919. It also reports a substantial

amount of new data based on the largest sample of femora used until that time. In the anthropological idiom and philosophy of the time in which it was compiled, the work succeeds to an impressive degree. In terms of the modern anthropological idiom, which is less particulate and more stringently attempts to define broad patterns and morphological complexes it succeeds less well. It is, nonetheless, a vast and immensely useful source book on "femoralogy".

The *Homo sapiens* femora gathered for this study consisted of material from two 17th century London plague pits: 700 femora from Whitechapel and 217 femora from Liverpool Street. A very wide variety of primates were also measured and these were classified only by genus; the sample size ranged from 2-18 femora, usually nearer to the lower figure. Forty-three measurements were obtained for each specimen and from various combinations of these parameters the same number of indices were formed. Data on a wide variety of human groups and specimens were extracted from the work of other authors; in some cases these data were grouped into racial categories which can at best be described as dubious. Certainly few workers today consider the Maori as "Australian" or the Andamanese as "Asiatics". A number of fossil hominids were included; these were

measured on casts and photographs when such were available; when these were not available, measurements were taken from published data. It scarcely seems excusable, however, to have measured the Galley Hill and Tilbury specimens from casts when the original material was in London.

Even though this is an exhaustive and detailed study, it can be criticized along several lines. The first concerns the sources of the comparative data other than the London sample. Although a large number of works were consulted in order to provide long lists of comparative data, no consideration was given to the anthropometric techniques used by these authors; this fact must severely limit the usefulness of many of the comparisons. For example, in a comparison of Platymeric Indices, Pearson and Bell used data from their own series, from Parsons and Hepburn (all of whom took the minimum antero-posterior diameter and then the transverse diameter at the same level) with that of Koganei (who took the measurements at 3 cm. below the lesser trochanter), with that of Martin (who took the maximum transverse diameter and then took the antero-posterior diameter at the same level).[1] Again, in a

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[1] See Section II.2.iii for a complete discussion of these osteometric techniques.

comparison of Pilastric Indices, they compared their own data (derived by taking the maximum antero-posterior diameter in the mid-shaft area, then the transverse at the same level), with that of Parsons (who took the maximum and minimum diameters wherever they occurred in the mid-shaft area), with that of Koganei (who took the diameters at the mid-shaft point). Similar criticisms can be made for their discussion of bowing and shaft obliquity. Moreover, they included data from a "modern French" sample of 60 specimens without recording how the measurements were obtained, or by whom.

A second criticism which can be made concerns Pearson and Bell's method of determining the sex of their London material. The plague pit material consisted of unassociated bones so they could not have had the advantages (which Warren for example had) of associated skull and post-cranial remains on which to base a total sexual pattern of the individual. Thus sex has been assigned "on a general anatomical appreciation" of the femur; there is however, a circularity in their discussion of how the sex was ascertained. The progression of logic seems to run: the bones are assigned to a sex because they show certain features, and the features of that sex are therefore defined on the basis of the included bones. No comparative material of

known sex was used in this study although such samples were available (see Warren 1897 and Parsons 1914). Therefore, the inescapable conclusion must be that the numerous correlations they calculated for character pairs involving sex are really correlations which may have very little to do with sexually discriminating features and may reflect more the general robusticity of the specimen. Correlations based on indices, however, are somewhat effective in reducing the size factor; the importance of some of their indicial correlation will be discussed in Section IV.

A third critical point must be made; this concerns Pearson and Bell's method of evaluating their data. This point, however, must be tempered with the knowledge that their evaluation represents perhaps the zenith of statistical practice of that day. Nevertheless, the demonstration of correlation or variation coefficients between character pairs does little to demonstrate the existence of wider morphological patterns.

Criticisms aside, there is a considerable amount of material of use to the present study. Their data on the obliquity of the femoral shaft is particularly relevant in view of the controversial and contradictory

results obtained for this parameter on some of the early Pleistocene hominids. Their measurement of this feature was made according to Broca's method[1] although Pearson and Bell severely criticized both the method and the instruments he used. They suggested that in view of the small mean range of shaft obliquity this feature must have faced heavy selective pressures during evolution. They added that the low values for this feature in "primogenial man are one of the few instances in which he is clearly closer to the apes than more recent men. In this respect the Trinil femur is not apelike and stands far closer to modern man than to the apes" (1919)

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[1] In Broca's method of measuring shaft obliquity, the femur was placed on the osteometric board with the goniometer attached. The bone would then have to be placed under the goniometer causing problems with both large and small bones. After orientation of the bone on the board, the degree of obliquity was read as the angle between the shaft axis (inadequately defined by Broca, according to Pearson and Bell) and the standard horizontal plane. The goniometer was placed so that it bisected the anterior surface of the bone at the points where the platymeric and popliteal indices were taken. The main source of error appeared to be parallax caused by the immovable goniometer.

In trying to draw their material together for their final conclusions Pearson and Bell constructed a "Simio-human mean". This consisted of plotting the mean values of certain parameters as a distance statistic for the gibbons, orang-utans, gorillas, chimpanzees, Simidae, 17th century Londoners, "*Pithecanthropus*" and Neandertal. The standard deviation of each group's variation from this "Simio-human mean" was then plotted. When the means and standard deviations are plotted for several femoral indices, for example, the result is a simple sort of univariate distance statistic.

Pearson and Bell conclude that "Recent Man is by far the closest of any member of the group to the Simio-human mean". From their data they argue that the nearest example of the anœstral type of human femur is to be found among the Cercopithecoidea since the femora of the Anthropoidea show a number of later specialisations. Thus "we put forward as a working hypothesis that the prot-simio-human femur was not a simple, straight, slender femur - a hylobatic femur developed for lightness and agility - but a troglodyte femur, robust, fossed for muscular attachments, and bowed, but without pilaster, in fact a much more human femur ... built for strength rather than agility". Thus in their metrical demonstration of a number of indicial similarities between the Simidae and the Hominidae, Pearson and Bell presage Kern and Straus' similar, but less well documented, suggestion.

Lagotala (1920) studied 100 femora from a 14th and 15th century cemetary at Geneva; the sample consisted of only male, right bones. In this study, in which he took the major shaft and proximal epiphyseal indices and three length measurements, he concluded that a long femur would have a smaller angle of obliquity than a short femur. He argued that the lengthening of the femur would be compensated for by a reduction in shaft obliquity and would thus result in a shorter neck - this would have the effect of making the flexors more efficient. Similar findings were reported by Pearson and Bell (1919) who were unable to find a significant correlation between oblique length, neck length or obliquity. Lagotala did not however give the data on which this conclusion was based nor did he give his techniques of measurement.

Ingalls (1924) reported a study on 100 femoral pairs from the Hamann Museum at Western Reserve University. These bones were taken from white males of known age; a total of 35 measurements was taken on each bone. He concluded that the older individuals showed "retrograde" (i.e. decreasing dimensions) changes in the general proportions of the femur; this was most pronounced in the epicondylar breadth. He noted that the overall femoral dimensions increase until about age 50 and thereafter a general decrease is seen in size. Additionally, "The oblique and trochanteric lengths

naturally run parallel, increasing steadily from the early thirties to the late forties, gaining about ½ inch during this period".

In describing the hominid remains from Broken Hill, Rhodesia, Pycraft (1928) provided some information on the femoral material from the site. Proximal and distal portions of a left femur, the proximal part of a right femur and a tibia were found in the cave. Because the right femur is 3 mm "larger" than the left, Pycraft described these as belonging to different individuals. His method of reconstructing the length of the left femur is unique. He examined a number of associated tibiae and femora until he found a tibia the length of the Rhodesian specimen; he then asserted that "one may assume this to be the length of the Rhodesian femur (477 mm) because the tibiae in these two have exactly the same length" (ibid) Pycraft regarded the straightness of the femoral shaft as a "Simian" feature although he did not record the degree of bowing or indeed if it was measured. He then stated that the individual must have walked with the legs wide apart and knees bowed! Moreover, he felt that the "peculiar features" of the skull were related in some (undefined) way to posture. The features of gait he described prompted him to name the specimen *"Cyphanthropus"* although Smith-Woodward had already proposed the name *"Homo rhodesiensis"* in 1921.

Le Gros Clark in the same year, pointed out that the attribution rested mainly on an erroneously reconstructed and orientated pelvis and suggested the new nomen be dropped.

Drennan (1929) described a femur associated with "An Australoid skull from the Cape Flats" which was said to strongly resemble the Galley Hill femora. He gave only the major shaft indices and calculated that the stature was either 5' 6" or 5' 7".

Keith (1931) mentioned a femur associated with the Fish Hoek remains; he suggested only that the height may have been about 5' 6".

Martin (1932) described a groove which sometimes occurs in the medial portion of the intercondyloid fossa. This groove was said to be caused by pressure from a tightly stretched posterior cruciate ligament during squatting; the groove was said to be "especially prevalent" in primitive peoples although his small sample of "early Irish" hardly seems ample to verify the point. This observation was also made by Siddifi (1934) on a sample of East Indians.

Walmsley (1933) defined the 3 axes of the femur: the mechanical, the anatomical and the load axes. The first runs from the centre of the head to the mid-condylar point;

the anatomical axis is plotted on a tracing and passes through as many possible centre points of the shaft and through the mid-condylar point. The load axis, runs from the centre point of the head and crosses the infracondylar plane at right angles. He pointed out that the anatomical and load axes in man usually intersect in the lower 1/3 of the shaft; however, he suggested that the higher this point of intersection, the more efficient will be the transmission of body weight. Thus a shaft, in which the point of intersection is high, can be more gracile than one where the point is low. In the robust Neandertal femora, for example, the point of intersection is just above the distal epiphyses. This does not apply to the anthropoids since their "uprightness" is locomotor and not postural and the human limb has been evolved for "static support". Walmsley concluded that "the full static functions of the femur were assumed ... in Neanthropic Man" and although the Neandertal femur had only limited static abilities "in this respect the *Pithecanthropus* femur is modern" (ibid). The implication here is that a bone with a large angle of shaft obliquity, in having a high point of axial intersection, should be more gracile. This does not seem to be the case with the highly angled and robust early Pleistocene hominid femora.

Arambourg, Boule, Vallois and Verneau (1934) investigated the human remains from Beni-Segoual (Mechta) Algeria. Of the 32 femora from the site, 28 were intact; they recorded only the three major shaft indices.

Beginning 1909 and extending throughout the thirties, Ales Hrdlicka made a number of contributions to the study of the femur. In general his work is characterized by a limited number of measurements and observations made on very large samples. His first study, (1909) on 116 Indians from Arkansas and Louisiana, recorded only "mean length" and the upper shaft diameters and included an observation on the development of the third trochanter. In one case, the third trochanter was seen to be in three parts, an unusual, if not unique, occurrence. In 1934, he began a series of studies on the shape of the femoral shaft. The first study (1934a) was made on a total sample of 10,667 femora from the United States National Museum. The sample included material from the Egyptian XII dynasty (n=200), "U.S.A. Whites" (n=1000), "Old Peruvians" (n=1139). A further 570 were neonates and foetuses and 961 were children and adolescents drawn from the same populations. In analysing this material he classified the mid-shaft cross section into round, elliptical plano-convex and prismatic. He found that the elliptical section at mid-shaft is most common in young children and the prismatic section is the most common in late adolescence and maturity. He finally

concluded that the shape of the shaft varied with age, side, sex, length and race but could offer no explanation for these changes. He particularly noted a correspondence between short femoral length and the cylindrical shape and between long femoral length with prismatic shape. No statistical evaluation of the material was attempted other than percentage values.

Hrdlicka later (1934b) provided additional data on the shape of the femur. In this study he included observations of the femora of lemurs (n=16), old world monkies (n=67), "American monkies" (n=59), Gorillas (n=144), Chimpanzees (n=156), Orangs (n=79) and Gibbons (n=38) plus 406 femora from Negro and White juveniles, adults and aged individuals and several fossil specimens. In this study he constructed several permutations of the original shaft shape categories: "near round", "near elliptical", and "indefinite" were included. From this vast amount of data gathered for these two studies he formulated three conclusions:

1) "No forms of the shaft of the femur occur in any of the primates that are not also found in man .. but man has several additional forms that are his alone, namely the plano-convex, the quadrilateral, the markedly fluted and the pilastered."

2) "In all the anthropoid and lower primates here dealt with the complex of the shapes of the shaft of the femur is simpler to much simpler than it is in man".

3) "... there is seen a gradual change in the shapes of the shaft with age ... The ultimate shape, may, it appears, be defined as the resultant of on one hand the inherited and largely phyletic, and on the other hand the ontogenetic factors that through the individual life have acted on the femur; or, more briefly, as the resultant of partly inherited and partly mechanical conditions." (1934b).

Thus the "flatness" of the gorilla shaft is "due mainly to the pressure exerted on the shaft by the thigh muscles" (ibid). Further explanation of the "mechanical conditions" which might affect shaft shape were not offered. Observations on a number of casts of fossil specimens were also made: the *"Pithecanthropus"* femur is said to be "rather indefinite , approaching somewhat the prismatic" the Neandertal femora were "near elliptical' ... (and) intermediate" (ibid). He later reiterated the position that development of crests and pilaster were "due mainly to ontogeny and not heredity" (1934c).

In an examination of 2150 "Old Peruvians" (1937-38) Hrdlicka came to the conclusion that flattening of the upper femoral shaft was due to "hereditary conditions" and was associated with platycnaemia and flattening of the humerus, however, "what is its value to the organism was not observed" (ibid). Hrdlicka took a total of six measurements on each specimen.

In 1938, Hrdlicka made a study of the occurrence of the third trochanter, a term he described as "inaccurate" and suggested instead the use of "gluteal tuberosity". He pointed out that this feature is present in the Perissodactlya, *Nycticebus* and some lemurs; it is absent in the Artiodactyla, most marsupials and the higher primates. He felt it was more often found in slender bones although it appeared in such strongly built bones such as Spy and Neandertal.

He concluded that the third trochanter occurs more often in "frail bones" and that there is a "faintly negative correlation of the pronounced ridge with pilastry and the same with platymery". He provided no data on "pilastry" or "platymery", however and his use of the term "correlation" must be taken in a subjective rather than a statistical sense.

OCCURRENCE OF THE GLUTEAL RIDGE IN NORTH AMERICAN INDIANS

	absent	slight	moderate to medium	above medium	nos.
♂ R	.96% n=8	15.71% n=131	36.45% n=304	5.76% n=48	491
♀ L	.82% n=9	9.83% n=84	38.71% n=331	9.94% n=85	509
♂ R	.20% n=2	12.76% n=128	33.50% n=336	6.48% n=65	531
♀ L	1.34% n=13	16.34% n=159	33.81% n=329	4.32% n=42	543

OCCURRENCE OF A GLUTEAL TUBERCLE IN NORTH AMERICAN INDIANS

Oblong Tubercle

	Small	Medium	Large
♂	6.87% n=116	21.67% n=366	8.05% n=136
♀	11.74% n=232	25.35% n=501	4.90% n=97

Rounded Tubercle

	Small	Medium	Large
♂	.53% n=9	3.26% n=55	.54% n=9
♀	.91% n=18	2.38% n=47	.20% n=4

Hrdlicka's data do not support his contention that more pronounced proximal gluteal markings occur in frail or female bones; the percentages rather describe a bell curve with maximum values occurring at the centre of the ranges.

Cameron (1934) suggested that the Anglo-Saxon limbs were transitional between "prehistoric man" and "modern" man" (i.e. 17th century Londoners). He felt that the "prehistoric type was produced by healthy, open air exercises coupled with swift and vigorous movements". He also felt that the platymeria is "no longer a feature of the modern British femur"; this feature was said to be "a symbol of unwonted strain ... during childhood" and that "bowing, pilastring and platymeria are ... more or less concomitant phenomena". He neither recorded his sample nor the figures on which he based his conclusions.

Pequart, Boulc and Vallois (1937) examined the remains of 12 males and 13 females from a Mesolithic site at Teviec. They reported that the femora showed marked platymeria and that the fossa hypotrochanterica was usually present but that the third trochanter was either absent or feebly developed. They provided only the major shaft indices.

In a report on the 29 individuals from Predmost, Czechoslovakia, Matiegka (1938) provided considerable data on the post cranial material but only mid-shaft and condylar measurements on the femora.

Buxton (1938) suggested a correlation between platymeria and platycnaemia, and between platymeria and mid-shaft flattening of the humerus. In his analysis of flattening of the upper femora shaft, Buxton suggested that such shape may increase the surface area available for muscle attachment without actually increasing the perimeter of the shaft itself. He postulated therefore, that such flattening may occur when there is a deficiency of bone material and that this deficiency may be due to nutritional factors. Buxton gave the following data for bones in the same skeleton:

COEFFICIENT CORRELATIONS BETWEEN "FLATTENING INDICES"

	femur and tibia	femur and humerus
L	+ .3579 (n=52)	-0.1759 (n=50)
R	+ .4441 (n=54)	-0.0639 (n=49)

(n= pairs)
(Buxton, 1938)

McCown and Keith (1939) examined the remains of 15 Late Pleistocene hominids from Mt. Carmel, Israel; 3 individuals were from the cave of Mugaret-et-Tabun and 12 came from the cave of Mugaret-es-Skhul. There were 3 femora from Tabun and 10 from Skhul. McCown and Keith made the assertion, apparently supported by the material, that there was a large degree of sexual dimorphism present in the specimens. If their sexual determination and stature reconstructions are reliable, the males stature ranged between 5' 8" and 5' 10"; the females between 5' 0" and 5' 4".

The most interesting femur from this sample is that from the Upper Acheulean layers in the Tabun cave and is termed "Ea", a reference to its stratigraphic position. This is reported to be 3/5 of a right proximal shaft from the base of the lesser trochanter to some distance past the mid-point; the specimen measures 225 mm. It is said to have been male, judging from its robusticity, but its estimated height of 5' 4" is less than that estimated for males in the upper levels. However, both height and sex estimations for so fragmentary a specimen must be doubtful. The specimen is said to be more mineralised than the femur of Tabun 1[1]. There are reportedly bony ridges or flanges on both the medial and lateral aspects of the Ea proximal shaft and the linea aspera is not elevated into a ridge. The indices are:

Platymeric Index	75.4
Pilastric Index	92.8

McCown and Keith said that the proximal ends of the specimen were x-rayed and that they were not "able to discern any

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[1] Tabun 1 reportedly had two right legs; one right femur is 'hearly complete"; the second right preserves only the distal half. They are both referred to a female of about 5' 0".

essential difference in trabecular structure". However, only x-rays of Skhul IV (left) and Tabun I (right) were reproduced; the quality of the x-rays is not sufficiently good to permit any opinions to be stated.

Vallois (1941-6) in a re-examination of the Chancelade material gave the major shaft indices and maximum length. He concluded that "l'homme de Chancelade n'est pas un Eskimo"; however, he provided no comparative data on what one might or might not expect of Eskimo post cranial material.

Stewart (1943) examined the skeletons of a large sample of Pre-Columbian Indians in Peru. He gave only a few measurements on the femur but reported on a "probable" case of syphilis in one specimen.

Townsley (1948) has held that his findings on immature material suggest that "the appearance of the adult type of (internal bone) architecture follows the

imposition of new forces on the femur due to weight bearing, walking and increased muscle contraction". This is in agreement with Carey (1929) and although not in opposition to the "trajectorial theory" adds a further dimension to that approach.

Evans (1952) tested the "ultimate tensile strength and percent elongation" from sections of the compacta of 7 adult males of known age and cause of death. The specimens, from subjects aged 47 to 81 years, showed the greatest tensile strength and energy absorbing capacity in the mid 1/3 of the femur; he concluded that the age of the individual had little effect on these capacities. His results also demonstrated that the tibia had the greatest tensile strength of the bones in the lower limb, and that the fibula also exceeded the femur in this respect.

Felts (1954) examined the femora of 53 foetuses and 1 infant and found that shaft obliquity decreases throughout development at the rate of .09° for every millimeter in increased length. The adult value would then be considerably less thanin the foetus. Torsion, conversely, generally increases with the length of the femur.

Cardini (1955) described a partial right femur from early Würm Mousterian layers in the cave of Santa Croce near Bisceglie, Italy. It was said to correspond very closely with known Neanderthal femora and was, therefore, attributed to that group. No measurements were given.

Tobin (1955) gave a detailed historical account of the development of theories relating to the structure of the proximal femur. He stated that Ward, in 1838, was among the first to describe the two major trabecular systems and was the first to note the occurrence of the trigonum internum femoris which has come to be called "Ward's triangle". Ward had likened the head of the femur to a street lamp bracket; Meyer and Culmann in 1866, (in Meyer, 1867) described it as a crane. Tobin also reviewed the controversy which arose from Wolff's Law, over whether tensile forces cause bone formation or resorption. He pointed out that Jensen especially had questioned whether tension and compression produced the same types of bone responses and suggested that muscle pull might affect bone as well. Finally Tobin described the trabecular structure of the proximal femur: the compressive lamellae arise from the medial cortex and the tensile lamellae arise from the lateral portions of the cortex and both systems intersect at right angles; part of this intersection comprises "Ward's triangle" which according to

Tobin is non-trabeculated due to "lack of dynamic stimulation".

Toerien (1955) in discussing the postcranial material associated with the Springbok Flats, South Africa, hominid remains pointed out the extreme length of the femora. The minimum reconstructed length of the femur was said to be 530 mm. The very robust lower limbs were reportedly associated with slender upper limbs; this pattern, according to Toerien, was "remarkably similar to some Cro-Magnon".

Defrise-Gussenhoven (1957) attempted to define a statistical generalised distance between a modern population and several fossil femora. Using a sample of 416 modern Belgians (some from the Congo) she separately plotted the mean population values for eleven parameters. Her formula was:

$$\Lambda^{2}_{p} = \sum_{i=1}^{p} \sum_{j=1}^{p} a^{ij} (m_i - d_i)(m_j - d_j)$$

Further when "Les parametres de la population n'etant pas connus nous estimons $^{2}_{p}$ avec la quantite":

$$L^{2}_{p} = \sum_{i=1}^{p} \sum_{j=1}^{p} a^{ij} (T_i - d_i) (T_j - d_j)$$

Thus:

(Λ_1^2) est $\delta(L_1^2)$

and

(Λ_2^2) est $\delta(L_2^2)$

and

(Λ_3^2) est $\delta(L_3^2)$ etc.

What the Λ^2 statistic demonstrated, then was not a multivariate distance but a univariate distance based on means and covariance matrices. The distance (D) was measured from the values for a fossil specimen to the centre (M) of the reference population.

It is difficult to evaluate her results since no fossil specimen showed uniformly or even predominately consistent Λ^2 values for all parameters. This paper would seem to be a complete rejection of the analytical approach inherent in the concept of a total morphological pattern and remains a reiteration, albeit with a modern slant, of the traditional univariate typological method.

Scott (1957) has related cortical thickness in the femur to the degree of muscular development and has stated

that cortical thinning with age may be related, in part, to muscular atrophy. He concluded, however, that other factors of a general constitutional nature may be involved in the rates of subperiosteal activity: sex hormones, nutrition and various environmental features may all influence the rates of bone growth.

Twiesselmann (1958) mentioned 3 femora from the Mesolithic site at Ishango. Of these, only one was complete enough to be measured; he gave the upper and mid-shaft diameters.

Schofield (1959) examined the femora from 92 adult Maori (total sample = 184 femora). He pointed out, as Turner had done, that the Maori femora are considerably platymeric and show pronounced medial and lateral flanges in the proximal portion of the shaft. He suggested as Manouvrier and Turner had, that the flatness of the upper part of the shaft is due to marked muscular development.

Wells (1959) reported on his re-examination of the Tilbury remains; he suggested that Owen's estimated length of 420 mm was "too short" and Keith's estimate of 446 mm was "too long". His own estimate of the reconstructed femoral length was between 430 and 440 mm.

Rossi (1961) reported on the discovery of a fragmentary femur from Sedia del Diavolo, near Rome. This fragment is

to be "certainly human and probably Neandertal" (trans. mine). No measurements or pictures were included.

The Neandertaloid femur of Fond-du-Fôret is the only femur to have been the sole subject of an entire monograph (Twiesselmann, 1961). It is not clear why the specimen was thought important enough to have been so treated since its considerable similarity to other Neandertaloid specimens (especially Spy) was recognized from the start. The upper epiphysis is missing but most of the shaft and the distal condyles are present. The analysis of this specimen and its comparison with other femora followed dogmatically traditional lines; the only acknowledgement of modern statistical methods being the inclusion of the means, standard deviations and coefficients of variation for the parameters of the comparative groups. This comparative data is drawn from a sample of 416 Modern Belgians and from a wide variety of data compiled by other workers. As was the case with Weidenreich and Pearson and Bell, parameters were compared with complete disregard for the methods used to obtain them. Twiesselmann concluded that the Neandertal specimens were very homogenous and confirmed Defrise-Gussenhoven's conclusion that the Neandertal femur "ne differe pas franchement de la population actuelle" (Twiesselmann, 1961).

Garden (1961) pointed out that the early comparison of the femur to a street lamp bracket (by Ward) and to a crane (by Culmann) was mechanically simplistic and failed to recognize the changing dynamics of stresses on the proximal femur. These stresses, he suggested, are mainly compressive although a considerable amount of tensile forces must obviously exist as well. Garden further suggested that at least part of the radiographic appearance of the proximal trabecular system is illusory and is caused by the spiral twist of the neck.

Atkinson, Weatherall and Weidmann (1962) reported on age changes in the cortex of the femur. Using a sample of 92 dissecting room specimens, they found that both cortical thickness and cortical density decreased with increasing age. Changes in bone density were said to be due to resorption of cortical material and not demineralisation. Changes in cortical thickness and bone density were evaluated by means of cross-sections taken from the diaphysis and metaphysis. In sections taken from the same bone it was found that the density was greater at the upper section, nearest mid-shaft than in the metaphysis. This discrepancy increased after the 5th decade and Atkinson et al. suggested that these density variations might be due to different rates of metabolic activity within the femur. They were not, however, able to correlate degrees of calcification (calcium/nitrogen ratios) with age and concluded that decreased density was due to increased resorption rather than demineralisation.

Brookes and Wardle (1962) investigated experimentally the effects of muscular imbalance on the proximal femur. The study was carried out on dissecting room femora and pelves with all but the relevant musculature removed; thus the attachment areas of ilio-psoas, gluteus medius and minimus and the adductors were maintained. They found that with pressure of 15 to 25 kg. applied only to the insertion area of ilio-psoas a valgus position of the head resulted. Lateral torsion of the neck and proximal shaft caused the lesser trochanter to assume a more antero-medial position than it had previously occupied. Weights of 9 to 15 kg. on the insertion areas of gluteus medius and minimus produced a varus condition of the head and neck; the resultant medial torsion caused the lesser trochanter to be placed in a relatively more posterior position. While this investigation dealt only with pathological cases of muscular imbalance the relationship and correlation between torsion, shaft angle and relative position of the lesser trochanter could be of some interest in studies of fossil hominids.

Davivongs (1963) examined 75 pairs of male and 55 pairs of female Australian aborigine femora. By recording the major shaft indices and epiphyseal diameters he was able to conclude that the aboriginal femur is more gracile than the modern English femur, as defined by Parsons and Holtby. He concurred with Parsons in the usefulness of the

femoral head dimensions in sexual discrimination. He stated that there was no marked difference from any group when the full range of variation is taken into consideration and that sexual differences were greater than ethnic differences.

Straus (1962) pointed out that although the Primates are one of the oldest Mammalian orders they are among the least specialised members of the class, except in the highly specialized development of the brain among some members of the group. He argued that the lack of specialisation is a characteristic of the femur of *"Proconsul"*, *Oreopithecus bambolii*, the Old World Monkeys and the Hominidae, in contrast with the more specialized femur of the Anthropoidea. This point of view has of course been put forward by others (Pearson and Bell, 1919; Kern and Straus, 1949). *Oreopithecus bambolii* reportedly further resembled the Hominidae in the high degree of shaft obliquity (which he does not record). He concluded that the "hominid femur was derived from one basically like those of Old World Monkeys in pattern, and that the pongid type of femur represents a divergent specialization".

Smith and Walker (1964) investigated the effects of ageing on the femoral cortex. They studied a group of

2030 females aged from 45 to 90 years. In order to do this they constructed a formula to measure cortical area:

$$\pi / 4 \ (2cd-c^2) = \text{Cortical Area}$$

Where c=sum of the medial and lateral cortical thicknesses at mid-shaft on the AP view and,

d=periosteal diameter at mid shaft on AP view.

This formula is valid for a true circle which the femoral section is not; moreover the anteroposterior diameters cannot be construed as being representative of all cortical diameters; the formula only examined the sum of these diameters taken from a single position, and discrete changes in either dimension were not considered.

They found that cortical area, so determined, increases with age although the actual cortical thickness decreased, i.e. periosteal apposition exceeded the rate of endosteal resorption.

Age	No.	Periosteal diameter at midshaft	Cortical thickness at midshaft	Cross-Section area
		(means with standard errors)		
45-49	286	31.32±0.15	18.67±0.17	644 mm^2
50-54	303	31.60±0.15	18.69±0.14	653 mm^2
55-59	501	31.86±0.13	18.17±0.12	652 mm^2
60-64	424	32.12±0.14	17.96±0.14	653 mm^2
65-69	291	32.85±0.16	18.08±0.16	678 mm^2
70-74	162	33.03±0.23	17.32±0.22	661 mm^2
75-79	63	34.74±0.32	17.68±0.37	718 mm^2

Smith and Walker concluded that the "outer accretion of femoral bone was 1.7 x faster than inner resorption" (ibid). However, in a smaller study which took samples from other parts of the femur they found less periosteal increase. Thus:

		PERIOSTEAL DIAMETERS		
Age	No.	Mid-shaft	Sub-trochanteric	Femoral Neck
45-59	30	31.03±0.50	34.20±0.52	35.91±0.42
75-90	30	34.63±0.39	35.95±0.35	36.85±0.39
increases		3.60	1.75	0.94
P =		<.001	<.01	<.10

They finally suggested that the increases in total shaft diameter were greater at mid-shaft because this would be the area of maximum "flexural stress" and this stress would stimulate the "periosteal accretion of bone".

Pauwels (1965) has studied the distribution of cancellous tissue in the femur in relation to the amount of stress applied to the bone. He assumed that since maximum stress is eccentrically applied to the femoral head during one-legged stance the total stress will be the product of body weight and the tension of the abductors; the maximum stress (and consequently the greatest radiographic density) should therefore occur at the point of intersection of these

forces at the axial centre of the femoral head. To test his hypothesis, Pauwels constructed an artifical hip joint and femur from transparent resin. In analysing the pressure loads with the aid of polarised light he found that the highest stresses occurred in the medial aspect of the neck, while minimum stress occurred in the area of Ward's Triangle. From this model Pauwels concluded that "it is incontestably clear that the density of the spongy tissue corresponds roughly at each point to the magnitude of the tensions affecting it ... Thus is the conclusion justified ... that the spongy tissue elements are stressed axially by pressure or by pulling"[1]. Pauwels' conclusions must be criticized on the same basis as those levelled at other proponents of the trajectorial theory: a single phase material such as resin will not resolve forces in the same way as heterogenous, multiple phase bone.

A femur associated with lower palaeolithic bifaces was reported from Fermé Bouassa, Morocco in 1966 (Rivallier, *in lit*, Oakley and Campbell, 1967). It was said to be possibly contemporaneous with the Swanscombe remains; no details were given and no further reports have been published.

Three human femora were reported from a site near the

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[1] Translated.

River Meuse at Beegden (Erdbrink and Tacoma 1966); one of these, belonging to a "large male" was said to date from the Middle Weichselian and may possibly be Cro-Magnon.

A fragmentary femur, consisting of the proximal 2/3 of a shaft with part of the neck has been reported from Anatolia. Erdbrink, Tacoma and Visser (1966) plotted the parameters of this specimen against Twiesselmann's (1961) results - they concluded that it seemed nearer to the Neandertals than to *Homo sapiens*. Vallois (1968) however maintained a guarded opinion with regard to the specimen's taxonomic affiliations; he did report that the compacta was very thick but gave no measurements to confirm this observation.

Trotter and Peterson (1967a and b) examined age changes in White females and 350 Negro females and found a positive correlation between maximum transverse shaft diameter and age ($P = <.01$). On the basis of linear regression figures they concluded that the increase was in the order of:

0.23 mm. per decade for Whites

0.27 mm. per decade for Negroes.

Their final conclusion was, however, that the "increase vanishes if corrected for cohorts"

The nature and degree of statistical contribution of the cohorts was examined by Trotter, Peterson and Wette in the following year when they examined the relationship between the transverse femoral diameter at mid-shaft with length, age and birth year. Their sample comprised 738 femora from Negro and White skeletons in the Terry Collection. They statistically evaluated the data through the procedure of multiple, partial regression coefficients in order to isolate the most contributory factor in the correlations between the variables. They found that although there is a statistically significant increase in the femoral diameter with age in all four groups (male and female, Negro and White) this may represent a secular trend rather than an individual, ontogenetic phenomenon. Trotter et al. argued that the older individuals are, by definition, from earlier birth years and the figures may thus represent a secular decrease in the femoral diameter through time. The figures further demonstrated a significant correlation between femoral diameter (positive) and between diameter and birth year (negative) but not with age at death.

Clark, Brothwell, Powers and Oakley (1968) reported the discovery of a further femoral fragment from the site of the original Rhodesian remains. The new fragment, which brought the total number of femoral fragments to five, had been discovered in 1921 but was not turned over to a museum

until some time later. The fragment represents the mid-shaft area of a right femur; its fluorine content is slightly lower than the previously known right femoral fragment but the uranium content of the two specimens is "identical". Clark et al, concluded that three or four individuals are represented by the known Rhodesian material.

McHenry (1968) reported on a study of radiopaque transverse lines in 102 femora of California Indians. He correlated the number of lines present in the femora with the three archaeological horizons at the site. Specimens from the lowest horizon, he stated had the greatest number of lines and the number of lines decreased in the upper horizons. McHenry suggested that this decrease was due to an increased and broadened subsistence efficiency; thereby implying that the lines are due to nutritional factors. This relationship has not been clinically demonstrated however. By dissection he found that the lines were caused by "disks of the dense cancellous bone extending across the entire marrow cavity". He further stated that the lines were about equal in males and females but did not discuss the accuracy of his sexual criteria.

Garn and Baby (1969) using a sample of 34 pairs of femora from Indian Knoll, examined the bilateral symmetry of radiopaque lines in the distal femur. Twenty-eight

pairs of the total sample demonstrated multiple radiopaque lines in the distal 1/3 of the bone; of these, 18 pairs showed one or more matching lines. Garn and Baby concluded that the lines reflect a systemic etiology rather than localised influences within the bone.

Van Gervan et al (1969) suggested that x-ray measurements to show cortical diameters may involve significant errors. In order to test this hypothesis, the authors measured femora from 23 female and 20 male Amerindian skeletons both by direct measurements of a bone section and by measurements of radiographic plates taken at the level of the section. They concluded that errors arose because radiography could not clearly distinguish the endosteal boundary and because the AP x-ray view did not always reflect the exact position where the direct measurement had been taken. They further stated that the increase of cortical porosity with age would further increase the error factor.

Their final results showed that measurements taken from x-rays over-estimated the amount of cortical loss due to age. The direct measurements showed a loss of 29.9% of the cortical thickness in females and 11.3% in males for ages over 42. In estimating the loss of cortical area, using the formula of Smith and Walker (1964) they found

that for the same age groups the males lost only 0.43% while the females lost 23.6%.

Percent of Bone Change from X-ray Measurement

		22-31	32-41	42+
cortical thickness	♂	0%	-14.89	-15.25
	♀	0%	- 2.99	-14.03
periosteal diameter	♂	0%	- 5.62	- 2.81
	♀	0%	+ 3.98	+ 3.19
cortical area	♂	0%	-16.34	-13.62
	♀	0%	+ 3.00	- 6.15

Percent of Bone Change from Direct Measurement

		22-31	32-41	42+
cortical thickness	♂	0%	- 5.60	-11.30
	♀	0%	-16.90	-29.90
periosteal diameter	♂	0%	+ 4.25	+6.38
	♀	0%	- 1.90	- 0.00
cortical area	♂	0%	+ 1.00	- 0.43
	♀	0%	-14.60	-23.60

(Van Gervan et al, 1969)

Day (1969) discussed a proximal femoral fragment recovered from Bed I or lower Bed II, Olduvai Gorge in 1959. This specimen, Olduvai Hominid 20, consists of the neck with the proximal portion of the shaft; the head is missing as is part of the lesser trochanter; the greater

trochanter is preserved. Day suggested that OH 20 is very similar to SK 82 and 97 from Swartkrans: the position of the lesser trochanter, the length of the neck, lack of lateral expansion on the greater trochanter, deep trochanteric fossa, absence of the trochanteric line and femoral tubercle, presence of a groove for obturator externus muscle are said to be similar in all three specimens. In discussing the functional significance of these features Day pointed out that the small size of the greater trochanter may indicate that gluteus medius and minimus may have been small and thus the pelvic tilt mechanism may have been less developed. However, the groove for the tendon of obturator externus on the posterior surface of the neck clearly indicates that hyperextension of the hip was possible and indeed habitual; thus at least some elements of the striding gait may have been present at this time. The lack of thickening along the intertrochanteric line may indicate, according to Day, that the ilio-femoral ligament did not function as it does in *Homo sapiens*. To account for the absence of a marked development of the ilio-femoral ligament, Day suggested that the individual's centre of gravity may have been anterior to that point in living man; thus the thickened ligament to counteract the posterior torque of the upper part of the body would not have been necessary.

Day concluded that "On the basis of these anatomical features it seems clear that the femur of OH 20 belongs to a robust as opposed to a gracile australopithecine" yet he provided no measurements for a gracile specimen nor did he state that he had examined any of the "gracile" specimens from Sterkfontein Moreover, while pointing out that OH 20 shows a number of concordant features with SK 82 and 97 he nevertheless stated "it would seem reasonable to allocate the new femoral fragment to *Australopithecus c.f. boisei*" (ibid). It would seem more reasonable to place the specimen in a group with which it had demonstrable similarity or to make no specific designation.

Suzuki and Takai (1970) reported on the hominid remains from the Amud cave site near Lake Tiberius; they are said to be those of a male, about 25 years old, and may date to the early or main Würm. Although 31 pages of this monograph were devoted to the study of the two femora very little important information about the specimens was recorded. The description rests largely of adjectival observations i.e. "larger, smaller" and very little anatomical information was conveyed. Moreover, the comparisons with other femora are based on data from other workers and the frequent criticism regarding the lack of true comparability of such parameters must be invoked again.

Suzuki and Takai concluded that the Amud femora are very like those from Mt. Carmel; they do not record however which Mt. Carmel femora the Amud specimens most resemble; they also stated that the bones bear some resemblance to the classic Neandertals.

After a preliminary report of a new investigation of the Cro-Magnon material (Vallois and Billy, 1965) the results of a complete re-investigation were published by Camps and Olivier (1970) considering both the anthropology and archaeology of the site. Billy, reporting in the 1970 volume, stated that the Cro-Magnon femur was remarkably robust and showed the development of a marked pilaster. The muscle markings of the proximal shaft, especially the fossa hypotrochanterica and "crete fessière" are extremely developed; the third trochanter, however, is absent.

A partial femur and os coxa OH 28 have been reported from the WK site, Bed IV, Olduvai Gorge. They were found on a "well-defined surface and lay 1.5 m apart" (M.D. Leakey, 1971). The boundary between the Matuyama Reversal and Brunhes Normal polarity episodes has been dated to about 0.7 m.y.; this level lies approximately at the base of Bed IV. Extrapolating from depositional rates in the Lemuta layer, Bed II, Leakey

has suggested that the top of Bed IV may be about 0.3 to 0.4 m.y. and the hominid fossils, near the middle of Bed IV may be dated to about 0.5 m.y. (ibid) The hominid material has been referred to *Homo erectus* by Day (1971) and he has suggested that the OH 28 femur is concordant in many features with the *Homo erectus* femora from Chou-kou-tien. In particular, he has pointed out the straightness of the shaft, low position of the least transverse diameter, convexity of the medial border, proximal continuation of the hypotrochanteric fossa and the thickness of the shaft walls. Nearly 500 stone artefacts from the WK site have been referred to the Acheulean complex (M.D. Leakey, 1971).

Armelagos, Mielke, Owen, van Gervan, Dewey and Mahler (1972) investigated the patterns of growth and age changes in the femora of a population of Nubians dating from 350 BC to 350 AD. This material was allocated to age categories on the basis of dental eruption; the criteria used for sexing was not given. Armelagos, et al. point out that although longitudinal bone growth ceases between 16 and 20 remodelling of the bone takes place throughout life; this remodelling involves absorption and redeposition of the bone tissue. Noting that while age changes in the femur have been the subject of a number of studies on living populations, no attempt has yet been made to

investigate these changes in archaeological material.

Their conclusions in part were

PERCENTAGE OF CORTICAL BONE LOSS IN MODERN POPULATION

	Male	Female
21-30	0%	0%
31-40	-5.0%	-14.0%
41-50	-8.0%	-9.0%
51-60	-10.0%	-17.0%
61-70	-12.0%	-28.0%
71-80	-10.0%	-31.0%
81-90	-12.0%	-40.0%

adapted by Armelagos et al from Bartley and Arnold 1965.

PERCENTAGE OF CORTICAL BONE LOSS IN NUBIAN POPULATION

	Male	Female
16-21	0%	0%
22-31	-6.25%	-6.25%
32-41	-5.00%	-18.00%
42-50+	-7.50%	-23.39%

(ibid)

(direct measurement, AP 8-9 cm below lesser trochanter)

Armelagos et al. concluded that there was a statistically significant relationship between females and cortical thickness ($P<0.001$) but the correlation

among males was not significant (P>0.25). A similar conclusion had been reached by Bartley and Arnold (1965). They further stated that since the greatest involution occurred in females aged 22-41 the involution was "not primarily a disorder of estrogenic hormonal etiology". They suggested that the earlier onset of cortical bone loss among Nubian females is due to "inadequate calcium intake and extended lactation". A similar study using the same populations and arriving at essentially the same conclusions was published by Dewey, Armelagos and Bartley in 1969. In examining the rates of cortical involution for each of the three Nubian groups they found no significant inter-group variations.

R. Leakey (1971) described three hominid femora recovered from the area east of Lake Rudolf, Kenya. Two specimens, KNM ER 736 and KNM ER 738, were tentatively attributed to *Australopithecus*; in a formal description of these specimens (Leakey, Mungai and Walker, 1972) this allocation was reaffirmed but no specific nomen has been suggested. KNM ER 738 has been attributed to *Australopithecus* apparently because of the similarity of its small head and long neck to other members of that genus, notably SK 82 and 97.

The reason for attributing the very robust femur KNM ER 736 to that genus is less clear.

A third specimen KNM ER 737, was said to resemble the "*Homo sapiens* femur in several respects" (Leakey 1971) but was not formally attributed to any taxon. Leakey did not clarify the ways in which the specimen resembled the sapient femur and indeed his description can be shown to be erroneous in several points: the supra-condylar lines are clearly apparent on the original specimen when there was said to be "no evidence" of them and the x-rays reveal considerable buttressing of the neck when this was also said to be absent.

Further femoral material has been reported from the Ileret area of East Rudolf (R. Leakey, 1972). A partial skeleton, KNM ER 803, containing a femoral shaft has been attributed to *Homo*; a very fragmentary femoral neck and proximal shaft, KNM ER 815, and a nearly complete diaphysis with the lower articular surface, KNM ER 993, were attributed to *Australopithecus*. As in the paper in the previous year, Leakey's taxonomic procedures are entirely subjectively based and no comparative data was provided on which to support his attributions.

Van Gervan (1972) has pointed out that most studies on human long bones have been orientated towards describing variation either between populations or between sexes and little attention has been given to the assessment of intra-population variability. In order to evaluate within-population variation Van Gervan performed a principal components and discriminant function analysis on the femora of 97 eleventh century Amerindians. The discriminant analysis confirmed that 98.4% of the femora had been correctly sexed by visual means. The principal components analysis showed that the highest eigenvalue (8.74) accounted for 51% of the variability; this first component reflected a general size factor. The second component showed a negative correlation between neck length and mid-shaft mediolateral diameter. However, the collo-diaphyseal and torsional angles showed positive correlation with each other but varied inversely with neck length and the mediolateral midshaft diameters. A third component showed that with increase in the collo-diaphyseal angle the degree of bowing and the subtrochanteric mediolateral diameter also increased. These features varied inversely with neck length, shaft torsion and bicondylar angle. Van Gervan suggested that this component was due to the activity of ilio-psoas and the glutei.

STATURE RECONSTRUCTION

II.2.i:

The first attempt to estimate stature from the length of the femur was made by Orfila in 1831 (cited by Telkka 1950). Carus (1854) developed a module approach for estimating the length of various parts of the body. One-third of the spinal column was said to equal one module; a "thigh bone" equalled 2½ modules and total body height equalled 9½ modules. Humphrey (1858) suggested that the proportion of the femur to the rest of the body was "nearly as 1:3½". He derived this proportion by measuring the long bones and body height of Europeans (n=25), Negroes (n=25), Chimpanzees (n=4), Gorillas (n=3), Orangutans (n=2) and various "dwarfs", "giants" and "extra cases". Topinard (1885) recognized sexual differences in stature. (Telkka 1950 and Keen 1953, provide a full discussion and bibliography on the development of the techniques of stature reconstruction). The basic fault with these early works is that in their primary investigations they took a certain stature as their datum point and worked backward to obtain the long bone lengths. This fault was recognized by Manouvrier (1892) who reworked Rollet's material and used bone lengths as a starting point and then proceeded to obtain estimates of stature.

Pearson (1899) noted that all previous workers had used fresh, undried bone and he therefore added a corrective factor for the small amount of shrinkage that occurs with desiccation. Pearson also introduced an element of statistical sophistication into the procedure by constructing regression formulae where the value of a component (a or b) in population B could be predicted from its value, in terms of standard deviations and correlations in population A. Pearson very optimistically suggested that there was a 95% chance of his estimated stature being within 3 inches of the actual measurement and a 50% chance that it was within 1 inch.

Pearson's formula is:

$$B = M_b = \frac{O_b}{O_a} r\ ab\ (A-M_a)$$

$$B = (M_b - \frac{O_b}{O_a} r\ ab\ M_a) = \frac{O_b}{O_a} r\ ab\ A$$

$$= C_1 + C_2\ A$$

When: C = the constants for the component

M = the means

O = the standard deviations

r = the coefficients of correlation

M_b = the mean of stature

M_a = the mean of a long bone (Pearson, 1899)

The main criticism of Pearson's approach is that he did not recognize that the proportional relationships of the long bones may differ between populations. This was recognized by Broca (1867) who was able to demonstrate variations in the intermembral indices of "Negroes" and "Europeans" and concluded that these variations were racial in origin. Regression formulae have more recently been constructed to deal with these population variations. Telkka (1950) provided data on the Finns and Dupertuis and Hadden (1951), noting that Pearson had only used data from short populations, constructed new regression formulae to deal with "Whites" and Negroes". Trotter and Gleser (1958) have utilized data from Mexican, Mongoloid and Puerto Rican groups and Genoves (1967) has given data on Meso-American populations. Keen (1953) added the critical point that Pearson had not made allowances for age changes in stature; he did not, however, provide data for these changes.

In sum then, criticisms have been made of stature reconstruction formulae on the basis of racial differences, age and generation changes, sexual differences and even sidedness (Telkka 1950). Nevertheless, virtually all works on fossil men have included estimates of living height based on long bone proportions or regression formulae which can have little validity in such a situation.

Stature reconstructions have even recently been made for certain australopithecines (Lovejoy and Heiple 1970) where not only do we not have complete limb bones but we have absolutely no information as to what proportion of total height these bones might have represented. Thus it is not surprising that Lovejoy and Heiple did not discuss how their estimate of 42 to 43 inches for *A. africanus* was obtained.

While some workers have dealt with reconstructions of stature from the long bones, others have attempted to reconstruct the length of fragmentary humeri and tibiae (Seitz, 1923) and humeri, tibiae and radii (Mueller 1935) are in the literature; only recently, however, has such data become available for the femur. Steele and McKern (1969) defined five points on the femur and gave the means and regression figures for the resultant four sections. Their sample, however, was confined to 117 pre-Columbian femora and cannot confidently be applied outside this group.

II.2.ii: REVIEW OF OSTEOMETRIC TECHNIQUES

LENGTH: The first study of femoral length was apparently made by Sue in 1755 (in Humphrey 1858). In this study the length of the foetal femur was measured at one month intervals throughout gestation; the femur was also measured during later development at 1, 3, 10, 14 and 25 years. He did not give his method of measurement. It was Broca, however, who in 1868 developed and formally proposed a series of measurements to indicate femoral length. Broca proposed 4 methods of obtaining femoral length, all taken on the "planche osteometrique".

1. Oblique length: with both condyles touching the vertical upright and the length read at the most distant point on the head. This is the most commonly used length measure since it most closely approaches the orientation of the femur in life.

2. Maximum length: with the internal condyle touching the vertical upright; the moveable block would record the maximum length on the head.

3. Maximum trochanteric length: with the internal condyle touching the vertical upright and the length read to the "top" of the greater trochanter.

4. Oblique trochanteric length: with both condyles touching the vertical upright and the length read to the "top" of the greater trochanter. (Broca, 1868 - in Topinard, 1885)

These four measurements were again proposed by Topinard (1885), and Pearson and Bell (1919). Further methods of measuring femoral length have also been proposed.

5. Trochanteric length: taken from the most posterior point on the external condyle to the "top" of the greater trochanter. (Klaatsch, 1900; Pearson and Bell, 1919).

6. Diaphyseal length: a projection method which uses a variation of the fundamental triangle. Here the length is taken from the intra-condylar point to the point where the long axis of the bone crosses the axis of the neck. The distal point of the long axis is taken midway between the points at which the condyles touch the horizontal plane; the shaft axis is then taken from the point to the "top" of the greater trochanter (Mikulicz, 1878).

7. Diaphyseal length: taken from the upper end of the spiral line to the mid-point on the proximal border of the patellar surface. This is taken with a tape (Bumuller, 1899)

8. Diaphyseal length: a projection method which uses the fundamental triangle from the mid-trochlear point to the coaxial point where the axis of the shaft crosses the axis of the neck (Pearson and Bell 1919). This is very similar to number 6 except for the position of the distal point of the shaft chord.

9. Diaphyseal length: from the uppermost point on the greater trochanter to the lowest point on the lateral condyle (Pearson and Bell, 1919; Gieseler, 1927).

10. Trochanteric length: uppermost projection of the greater trochanter from the point of intersection of the proximal shaft with the base of the greater trochanter (Gieseler, 1927).

11. Proximal Epiphyseal length: from the middle of the head to the middle of the intercondyloid fossa (Martin 1928 no. 2a).

12. Diaphyseal length: from the uppermost point of the greater trochanter to the lowest point on the medial condyle (Martin, 1928 no. 3).

13. Diaphyseal length: from the lowermost point on the greater trochanter to a line drawn horizontally from the most proximal point of the distal articular surface (No. 5, Martin 1928).

14. Diaphyseal length: from the quadrate tubercle (Tuberculum linae obliquae) to the middle of the distal intercondyloid line (no. 5a, Martin 1928).

A large number of indices have been proposed which show a relationship between femoral length and various diaphyseal measurements.

1. Bicondylar Trochanteric Index:

$$\frac{100 \times \text{trochanteric length (no. 5)}^{1}}{\text{bicondylar width}}$$ (Klaatsch, 1900)[2]

2. Proximal Epiphyseal Index:

$$\frac{100 \times \text{breadth of proximal epiphysis}}{\text{trochanteric length (no.5)}}$$ (Klaatsch, 1910)

3. Distal Epiphyseal Index:

$$\frac{100 \times \text{breadth of distal epiphysis}}{\text{trochanteric length (no.5)}}$$ (ibid)

4. Condylar length Index

$$\frac{100 \times \text{length of external condyle}}{\text{trochanteric length (no.5)}}$$ (ibid)

5. Index of Transverse Slenderness

$$\frac{100 \times \text{pilastric transverse diameter}}{\text{length (no. 6)}}$$ (Pearson & Bell, 1919)

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[1] The numbers given in brackets refer to length measurements as described in the previous section.

[2] A similar index was proposed by Pearson & Bell (1919) although they inverted the ratio.

6. Index of Sagittal Slenderness:

$$\frac{100 \times \text{pilastric AP diameter}}{\text{length (no. 4)}}$$ (ibid)

7. Direct-Oblique Length Index:

$$\frac{100 \times \text{trochanteric length (no. 1)}}{\text{maximum length (no. 2)}}$$ (ibid)

8. Direct-Oblique Trochanteric Length Index

$$\frac{100 \times \text{trochanteric length (no. 9)}}{\text{direct length (no. 4)}}$$ (ibid)

9. Secondary Capital Index:

$$\frac{100 \times \text{vertical + AP head diameters}}{\text{length (no. 1)}}$$ (ibid)

10. Primary Capito-Collar Longitudinal Index:

$$\frac{100 \times \text{capito-collar length}^{1}}{\text{length (no. 1)}}$$ (ibid)

11. Secondary Capito-Collar Longitudinal Index:

$$\frac{100 \times \text{capito-collar length}}{\text{length (no. 3)}}$$ (ibid)

12. Condylar Trochanteric Index:

$$\frac{100 \times \text{external condylar length}}{\text{length (no. 5)}}$$ (ibid)

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[1] The capito-collar length represents the distance between the centre point of the head and the point of intersection of the centre axes of the neck and shaft.

13. Index of Robusticity:

$$\frac{100 \times \text{AP} + \text{transverse pilastric diameters}}{\text{length (no. 3)}}$$ (ibid)

14. Robusticity of Head Index:

$$\frac{100 \times \text{vertical} + \text{horizontal head diameters}}{\text{length (no. 3)}}$$ (ibid)

15. Popliteal Shaft Index:

$$\frac{100 \times \text{popliteal length}}{\text{length (no. 6)}}$$ (ibid)

The relationship between the sub-trochanteric measurements is reflected in the Platymeric Index first proposed by Manouvrier:

Platymeric Index:

$$\frac{\text{Sub-trochanteric AP diameter} \times 100}{\text{Sub-trochanteric transverse diameter}}$$ (Manouvrier 1899)

Martin (1928) also used this index; as he took a transverse maximum, his method of measuring will result in indices slightly higher than those of Manouvrier. Although Manouvrier's index is the one most commonly used, several other formulae have been proposed in the past-

Platymeric Index:

$$\frac{\text{Minimum upper diameter} \times 100}{\text{Maximum upper diameter}}$$ (Hrdlicka, 1916).

Hrdlicka continued to use this formula (1930, 1938) and was followed in this by Stewart (1935). Neither worker specified the orientation of the "minimum" and "maximum" diameters or even if they were to be taken at the same level. Hrdlicka later sought to clarify this point and suggested a new formula:

Platymeric Index:

$$\frac{\text{Maximum transverse diameter in the upper part of the flattening}}{\text{Minimum AP diameter in the upper part of the flattening}}$$

(Hrdlicka, 1939)

This method has also been used by Stewart (1943) and Romero et al (1949).

The numerical definitions of the degrees of platymeria differ with various workers. In Martin's terms:

Hyperplatymeria = <74.9
Platymeria = 75.0 - 84.9
Eurymeria = 85.0 - 99.0
Stenomeria = >100.0

(Martin, 1928)

Manouvrier defined:

Sagittal Platymeria = <80.0
Absence of Platymeria = 80.0 - 100.0
Transverse Platymeria = >100.0

(Manouvrier, 1889)

Manouvrier's last categories correspond to Lehman-Nitsche's (1895) Platymeric, Eurymeric and Stenomeric indices respectively.

The word "Platymeria" received a wider application

by Weidenreich (1938) and by Weidenreich and von Koenigswald (1939). Weidenreich (1938) discussed the "Platymeria" of the popliteal surface in *"Pithecanthropus"I* and Weidenreich and von Koenigswald (1939) mentioned the "Platymeria" of the Solo tibiae. In both cases these are unique applications of the word.

MID-SHAFT MEASUREMENTS: The first discussion of mid-shaft measurements and indices was by Broca (1868) who formulated the "Indice Femoral". Topinard (1885) renamed it the Indice de La Section du Femur:

$$\frac{\text{Maximum AP diameter} \times 100}{\text{Transverse diameter}}$$ (Topinard, 1885)

The vertical orientation of these measurements is not given but the discussion would seem to suggest that they be taken at mid-shaft (ibid). This point was later clarified by Berteaux (1891) who suggested a Pilastrique Index:

$$\frac{\text{AP diameter at the mid-point} \times 100}{\text{Transverse diameter at the mid point}}$$ (Berteaux, 1891)

This technique was followed by Bumuller, 1899; Hepburn 1897b; Bello y Rodgriguez 1909; Ingalls, 1924; Martin 1928; Arambourg et al, 1934. Kuhff (1875) proposed taking the pilastric measurements at the level of the nutrient foramen; this would be virtually useless, however, since the position of the foramen is extremely variable.

Parsons (1914) proposed taking a maximum anteroposterior and then a minimum transverse measurement wherever they occur in the mid-shaft area not necessarily at the same level. This technique was followed by Tamagnini and De Campos (1916).

Weidenreich did not specify his technique of measurement other than "mid-shaft" (1941). Although Weidenreich used Martin's methods (1928) for certain techniques and indices, Martin proposed two quite different mid-shaft indices (ibid) and so Weidenreich's precise method of determining the Pilastric Index remains in doubt.

Pearson & Bell proposed a
Pilastric Index:

$$\frac{\text{Maximum AP in mid-shaft area} \times 100}{\text{Transverse diameter at same level}}$$

(Pearson & Bell 1919)

They stressed that the maximum anteroposterior measurement should be taken wherever it occurred in the mid-shaft region; the transverse diameter must be taken in the same vertical plane but not necessarily at right angles to the anteroposterior diameter. Martin (1928) suggested the same formula as Pearson and Bell and stipulated that the anteroposterior diameter should be taken at the point of the highest elevation of the linea aspera.

As they did with the Platymeric Indices, American anthropologists have followed a somewhat independent line with mid-shaft indices.

Hrdlicka proposed the:

Index of the Shaft:

$$\frac{\text{Transverse diameter at the middle} \times 100}{\text{AP diameter at middle}}$$ (Hrdlicka 1916)

This was used also by Stewart (1935, 1943); Hooton (1930) and again by Hrdlicka (1939).

Romero proposed a formula later used by Broste (1956):

Index at the Middle:

$$\frac{\text{Maximum diameter at middle}}{\text{Minimum diameter at middle}}$$ (Romero, 1949)

Pearson and Bell (1919) recognized that because of pilaster formation in some bones, specimens of quite different shape might demonstrate similar indices. They, thus, introduced three new indices in order to demonstrate more clearly the degree of pilaster formation and the shape of the mid-femoral shaft.

(a) Index of the Linea Aspera:

$$\frac{\text{Breadth of Linea Aspera} \times 100}{\text{AP diameter at mid shaft}}$$ (Pearson & Bell 1919)

The"breadth of the linea aspera" is the distance between the medial and lateral lips of the linea aspera at mid-shaft level.

(b) Ellipto-Pilastric Index: Let a circle with the AP diameter at mid-shaft equal the diameter of the circle; let the area of this circle = C; take A to be the area of the mid-shaft cross-section read with a planimeter. If there is significant pilastric formation C will be greater than A; if pilastric formation is minimal then A will be greater than C. The index is:

$$\frac{C \times 100}{A}$$ (ibid)

(c) Third-point Pilastric Index: This index was discussed in general terms but the method of its determination was not given. From the context of the discussion it may be surmised that the AP and transverse diameters are taken at 1/3 of the femoral length, but whether this is 1/3 from the top or bottom, using oblique or absolute length is not clear. (ibid).

LOWER SHAFT MEASUREMENTS: Various methods of measuring the distal shaft have been described. The "Popliteal Index" was first described by Manouvrier (1895) in order to demonstrate how the "*Pithecanthropus" I* femur differed from other femora at the distal end. He defined two antero-posterior measurements at the lower end. The "direct AP" measurement was taken from the highest point "m" on the distal anterior surface, in the standard vertical plane, to a midpoint "p" on the posterior or popliteal surface. The point "p" was defined as being equidistant from the supra-condylar lines, also in the standard vertical plane.

Thus, the line "mp" was approximately at right angles to a line horizontal to the plane of the base of the condyles. The "oblique AP" diameter was taken from point "m" to a point "n" on the external supracondylar line in the vertical plane. Manouvrier also stated that when "mp" is greater than "mn" the femur will have a convex popliteal surface such as *"Pithecanthropus" I.* This is true in this case but Pearson & Bell (1919) show other femora in which "mp" is greater than "mn" but which are concave. Although exceptions may be noted, they point out the general ability of the "Primary" Popliteal Index (defined below) to indicate concavity or convexity. Furthermore, concave popliteal surfaces generally have lower indices and there is a gradual increase through flat to convex surfaces, which have the highest indices.

Hepburn's (1897a) conclusions were very similar to those of Pearson and Bell. While recognizing that "High popliteal indices do not of necessity imply a convex surface in this region" he nevertheless based his evaluation of this area of the measurements "mp" and "mn".

In describing his method of taking the "mn" and "mp" measurements, Hepburn makes no mention of the vertical orientation of the measurements, (1897b). This is worthy of mention since the differences between "mp" and "mn" in 6 out of 25 specimens is 0.5 mm. It is

of further interest that in two papers discussing, in part, the Trinil femur, Hepburn failed to give the "mn" measurement for this bone (1897a, b).

Manouvrier (1895a) suggested measuring popliteal width at 4 cm. above the highest point of the condyles on the anterosuperior articular surface. He was followed in this method by Hepburn (1897b), Pearson and Bell (1919) and Martin (1928). Manouvrier felt that the 4 cm. position might be slightly increased or decreased to deal with long or short bones. Klaatsch (1900) proposed taking this measurement at 2 cm. above the articular surface since this might, in his opinion, separate the Trinil femur more clearly from other femora. Pearson and Bell (1919) criticized the 2 cm. position because they stated that it would not adequately discriminate between concave and convex popliteal surfaces and suggested that Manouvrier's 4 cm. position might be more useful in this regard. It is obvious, however, that neither position alone can describe the curvature of the intervening popliteal surface; an index reflects the relationships between the measurements and will therefore never consistently reflect the shape of the shaft.

The relationship of the distal shaft measurements was first described by Manouvrier (1895):

$$\text{Popliteal Index (Manouvrier 1895)} = \frac{\text{100 mp at 4 cm.}}{\text{Popliteal width}}$$

Primary Popliteal Index = $\frac{\text{100 mp at 4 cm}}{\text{Popliteal width}}$
(Pearson & Bell 1919)

Indice Popliteal = $\frac{\text{100 mp at 4 cm}}{\text{Popliteal width}}$
(Arambourg et al, 1934)

Although Martin did not distinguish between "mp" and "mn" his sagittal measurement (no. 11) corresponds roughly to Manouvrier's "mn". He gives the Popliteal Index:

$$\frac{\text{Least Lower Sagittal Thickness (at 4 cm) x 100}}{\text{Lower Transverse Thickness (at same level)}} = \text{"mp"}$$

(Martin, 1928)

A number of workers have proposed other ways of measuring and describing the distal end of the femur. Hepburn (1897b) suggested measuring popliteal length "from the posterior aspect of the external condyle upwards to the point at which it could be definitely determined that the margins of the linea aspera were diverging from each other". While he recognized that the point of divergence may be variable and imprecise he felt that the amount of error would "never be so great as to invalidate the value of the measurement" (ibid). Klaatsch (op. cit.) felt that popliteal length was so difficult to measure accurately that he favoured dispensing with the measurement altogether.

Indices which reflect the various measurements of the distal shaft have been proposed as follows:

1. Popliteal Index:

   $\frac{\text{width (at 4 cm) x 100}}{\text{maximum bicondylar width}}$ (Hepburn, 1897b)[1]

2. Sagittal Index of the Lower Shaft:

   $\frac{\text{100 x least lower sagittal diameter}}{\text{sagittal diameter at mid shaft}}$ (Martin, 1928)

3. Popliteal Length Index:

   $\frac{\text{popliteal width at 4 cm.}}{\text{popliteal length}^2}$ (Pearson & Bell 1919)

4. Index of Popliteal Skewness:

   $\frac{\text{100 x direct AP diameter of lower shaft}}{\text{oblique AP diameter of lower shaft}}$ (ibid)

5. Pyramidal Popliteal Index:

   $\frac{\text{100 x popliteal width}}{\text{popliteal length}}$ (Ibid)

6. Transverse Index of the Lower Shaft:

   $\frac{\text{lower transverse diameter x 100}}{\text{transverse diameter at midshaft}}$ (Martin, 1928)

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[1]This has been referred to as the "Soffit Index" by Pearson and Bell.

[2]Popliteal length is taken from the point of divergence of the linea aspera to the centre of the intercondylar line.

7. Femoral Bièpicondylién Indice:

$$\frac{10 \times \text{trochanteric length}}{\text{biepicondylar breadth}}$$ (Vallois, 1919)

8. Indice Femoro-Condylién Externe:

$$\frac{10 \times \text{femoral length}^1}{\text{maximum AP diameter of the external condyle}}$$ (ibid)

Bowing: The metrical description of the anteroposterior curvature of the human femur was first attempted by Kuhff (1875). His method was to take the highest point on the anterior surface of the shaft above the horizontal plane on which it lay. The maximum height of this arc above the vertical plane was measured, giving the subtense. He was followed in this method by Berteaux (1891); and Parsons (1913). The inherent fault in this method, unrecognized by those who used it, is the effect of the size of the condyles on the height of the arc. Large condyles will obviously raise the anterior surface and increase the length of the subtense. Evangeli-Tramond (1894) measured the height of the maximum curve of the linea aspera above the standard vertical plane and here again the same criticism must apply. Lehman-Nitsche (1895), followed the osteometric technique of Kuhff and constructed an Index of Bowing:

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[1]Vallois did not state how this length was to be measured.

$$\frac{\text{Highest point on the anterior surface} \times 100}{\text{Maximum trochanteric length}}$$

"Bumuller (1899 in Pearson and Bell 1919) placed the bone on its lateral surface on an osteometric board with the posterior aspect against the lateral upright. With a rule placed on the anterior face of the bone in the sub-trochanteric area, and parallel with the long axis of the bone, the angle between this tangent and the lateral upright could be read to give an indication of the extent of the bowing. This will, however, give no indication of the bowing in the centre of the shaft.

Guldberg (1905) used a method of projecting the curve of the anterior surface and then measured the maximum subtense. He did not, however, define the upper and lower limits of the chord. Antony and Rivet (1907) measured the curve of the anterior face from epiphysis to epiphysis as a chord and then found the maximum subtense of this arc to a vertical plane. They calculated a "radius of curvature" as follows:

$$R = \frac{(C^2 + 4f^2)}{8f}$$

where C = chord

f = subtense (Antony and Rivet, 1907)

As Pearson and Bell (1919) pointed out this formula is true only for a true arc and will not take into account the flattening near the epiphyses.

Parsons (1913) followed the osteometric method of Kuhff; Parsons, however, added the precaution of laying the bone near the edge of the table so that the calipers could be braced against the table edge, therby assuring an accurate vertical orientation. From the measurements he constructed an index:

Index of Bowing:

$$\frac{\text{Maximum distance of the subtense to the vertical plane}}{\text{Oblique length}}$$

(Parsons, 1913)

Pearson and Bell (1919) like Guldberg, advocated a projection method but in this case the centroids of the upper, middle and lower sections of the femur were located and plotted in a plane perpendicular to both the horizontal and vertical plane. A chord was then taken from the platymeric cross section to the popliteal cross section and the maximum subtense was thus defined. Their index was:

Index of Bowing:

$$\frac{100 \times \text{Subtense}}{\text{Chord Length}}$$

(Pearson and Bell, 1919)

They constructed a further index in order to demonstrate the position of the maximum subtense in relation to the chord length. Thus:

Secondary Index of Bowing:

$$\frac{100}{\text{Distance from the foot of the Subtense to the Popliteal End of the Chord}}$$

(Pearson and Bell, 1919).

Reid took two chords in order to determine the bowing of the femur (1927). One was taken on the front of the shaft over the extent of the curve; the second was taken between the end points of this curve. The highest point on the "chord of curvature" defined the extent of the bowing. Reid thus formed the:

Index of Curvature:

$$\frac{\text{Height of the Shaft Curvature}}{\text{Length of the Chord of the Curve}}$$ (Reid, 1927).

This index has also been used by Martin (1928).

Weidenreich (1941) followed Reid's methods in measuring the bowing of *"Sinanthropus"* but found it necessary to alter his "Lageindex I" since the distal portion is missing on all the Peking femora. His modification of the "Lageindex I" consisted of substituting the "proximal terminal point" (ibid) for the distal point. Weidenreich's "Bending of the Femur Shaft" thus reflects the relationship between the subtense and the proximal termination of the chord.

McCown & Keith (1937) used Martin's method but slightly altered the orientation of the femur so that a "true horizontal" was obtained in the projection. In order to do this the proximal end was raised so that the proximal terminal point of the arc was at the same level as the distal termination point of the arc.

II.3.i: China: The first hominid specimens from the Locality I site were recognised in 1926 by Otto Zdansky. Two teeth, a right upper molar and a lower deciduous premolar, were identified in material which had been excavated in 1920; the specimens were then at Uppsala University. The molar was so worn that the "cusps were almost obliterated" and had a single root which resulted from the fusion of three roots; Zdansky saw this as significant since "all anthropoid apes possess three distinct roots. In man, all the three molars can have fused roots" (Zdansky, 1927). Because of the fusion of roots and general conformation he allocated the two teeth to *"Homo sp."*. A third tooth was found, *in situ*, at Locality I on October 16th, 1927 by Dr. Bohlin in Layer I (Black 1927); however, this tooth is reported elsewhere to have come from Layer V (Black et al, 1933). This tooth was a slightly worn lower first molar. In studying this tooth Black (1927) stated that he recognized considerable similarity between the two teeth described Zdansky and this new, third tooth nevertheless he allocated this tooth to a new taxon because of its "unique character and great antiquity". The name *"Sinanthropus pekinensis"* had been informally suggested by A.W. Grabau and was now formally proposed by Black (1927).

By the late 1930's many workers had remarked on the similarities between the *"Sinanthropus"* and *"Pithecanthropus"* crania although several had also noted differences in the femora of the two groups (Weidenreich, 1938, 1940, 1945; von Koenigswald and Weidenreich, 1939; Le Gros Clark, 1940 and later; Day, 1971).

Le Gros Clark's position on the femoral differences in 1940 is notable, however. He stated "The authors (von Koenigswald and Weidenreich) use the remarkable argument that, because 'the femora ascribed to *"Pithecanthropus"* of Java show a marked degree of platymeria such as is not found in the femora of *"Sinanthropus"*, therefore they probably do not belong to *"Pithecanthropus"* ... A similar process of reasoning would also lead to the conclusion that, because a femur excavated from a Neolithic barrow shows more platymeria than the femur of a modern Englishman, therefore it cannot belong to *Homo sapiens*!" (1940). It seems that Le Gros Clark misunderstood both the features of the specimens involved and the arguments of the authors he was criticising.

Although Boule credited himself with being the first to suggest taxonomic synonomy of the Javan and

Chinese specimens in 1929, at that time he actually suggested that *"Sinanthropus"* was a transitional form between *"Pithecanthropus"* and Neandertal (Boule and Vallois, 1957). Weinert (1931) appears to have been the first to suggest this generic identity and he proposed the name *"Pithecanthropus sinensis"* although he earlier (1928) had suggested that *Pithecanthropus* might be included within the genus *Homo*. *"Pithecanthropus sinensis"* was later accepted by Piveteau (1957). Eikstedt (1932) also recognized the general similarity of the Asian hominids of this period and proposed the nomen *"Praehomo asiaticus"* with sub-specific classifications of *"sinensis"* and *"javanensis"*. Hennig, in the same year, showed general agreement with Black but demonstrated a degree of uncertainty by proposing *"Sinanthropus (Pithecanthropus?) pekingensis"*. Zuckerman (1933) while postulating that *"Pithecanthropus"* and *"Sinanthropus"* (with Neandertal and *"Eoanthropus"*) were, as a group, more similar to each other than to modern man, did not favour including them within a single genus. Instead he proposed a revision of the family Hominidae to include two sub-families: the Palaeanthropidae and the Neanthropidae, a suggestion he attributed to Elliot Smith. The Palaeanthropidae would include "archaic types" such as*"Pithecanthropus"* and *"Sinanthropus"*.

A number of workers accepted the co-generic status of the Chinese and Javan material but did not suggest a genus to contain the specimens (Le Gros Clark, 1937; Osman-Hill, 1940; Zuckerman, 1940; Simpson, 1945; Weidenreich, 1946). Le Gros Clark (1940) proposed *"Pithecanthropus pekinensis"* with sub-specific nomina to denote racial status; this has subsequently been used by Boule and Vallois (1952), although they have continued to use *"Sinanthropus"* elsewhere (1957).

Weidenreich's opinion of the relationship between *"Pithecanthropus"* and *"Sinanthropus"* is somewhat equivocal. Early in his comparative work on the two groups he decided that *"Sinanthropus"* had to be considered as representing a more primitive type than *"Pithecanthropus"* (1937); although later (1938 and 1939) felt that the two specimens had attained "the same general stage of evolution" (1939). In 1939 he allocated *"Pithecanthropus"* and *"Sinanthropus"* to the same taxon *"Homo primigenius"*. However, in 1940, Weidenreich proposed that *Pithecanthropus* and *Sinanthropus* should be designated as *Homo erectus* with sub-specific nomina of *H.e. javenensis* and *H.e. pekinensis* (or *sinensis*). Later he reaffirmed this position but a close examination of the Introduction (Weidenreich 1941) indicates that he was none too clear about taxonomy, its purpose or its meaning. He restated the allocation to *Homo erectus* and continued: "I believe .... that all known hominids belong to one and the same species. If we adhere to Linnaeus' term *Homo sapiens* as the

definite name of the human species, then the designation *Homo erectus* should logically be altered into *"Homo sapiens erectus"* (1941). He concluded "I prefer, therefore, to adhere for the present to the old practice and continue to call *Sinanthropus "Sinanthropus"* and *Pithecanthropus "Pithecanthropus"* (ibid). He has been followed in this by Boule and Vallois (1957). In 1943 Weidenreich stated that "The names given to groups and sub-groups of fossil hominids have no "generic" or "specific" meaning. They are nothing but convenient labels" (1943); he did not use the nomen *Homo erectus* after that date.

The only full report on the Chou-kou-tien post cranial remains is Weidenreich's original description published in 1941. The original fossil material is presumed to have been lost in the early 1940's and although casts of the specimens were made in Peking these have not been widely available; consequently the literature concerning personal examination of the Chinese post-cranial material is virtually limited to the original monograph.

Weidenreich's discussion of the characteristics of the Chou-kou-tien femora demonstrated considerable confusion and contains numerous contradictions and some inaccuracies and because of these factors any summary statement regarding this work is impossible.

Although it is acknowledged both by Weidenreich and the present author that it is the combination of morphological features which is most important in any analysis, for the purposes of critical examination each of Weidenreich's suggested characteristics of the Chou-kou-tien femora will be analysed separately.

Constrained as he was by geography and an uncertain political situation, Weidenreich's comparative modern sample consisted of only Mongoloids, a few Amerindians, and 7 Australians. No other modern racial groups were included. Four groups of primates were also used for comparison: Gorilla, Chimpanzee, Orang-utan and Siamang; all data on primates was taken from a single source (Pearson and Bell, 1919). The variety of fossil material used for comparative purposes was, however, impressive: Predmost, Ordos, Mechta, Mt. Carmel (the site is not always recorded) the Upper Cave specimens from Chou-kou-tien, "Pithecanthropus" I to IV, various early Chinese specimens and a number of Neanderthaloids such as Ehringsdorf, Spy, Krapina, La Quina, La Ferrassie and Neandertal. Weidenreich did not, of course, have personal access to all of this fossil material and in most cases simply records measurements taken from publications. As will be demonstrated, his comparative material is, for a variety of reasons, somewhat unreliable.

Weidenreich summarised his description of the seven Chou-kou-tien femora by stating "The femur is identical with a human femur in size, form, proportions, and character of the muscular markings, differing in all these features from the anthropoid thigh bone in much the same way as any human femur. It possesses nevertheless several peculiarities which place it in a singular position in the variety of human femora" (1941):

1. The *Sinanthropus* femur is relatively short". Elsewhere, however, he stated that "The Sinanthropus femur does not differ in length and robusticity from that of modern man" (ibid). Only two of the femora preserve even half of their original length (Femur I (♂)=199 mm. and Femur IV (♂)=312 mm.) and it is therefore clear that Weidenreich could not make a definite assessment of the population variability of femoral length. Nevertheless, his estimates of the reconstructed oblique lengths of two of the femora (Femur I = c. 400 mm. and Femur IV = c. 407 mm.) are lower than the mean of Pearson and Bell's (1919) data for the oblique length of male femora (435.5 mm) and above their figures for females (398.5 mm).

2. The femora were said to be "slightly bent forward (and) the vertex of the curvature is situated below the middle of the shaft" (1941).

Anteroposterior bowing of the shaft could be measured only on Femur IV although its presence was observed on Femur I. Weidenreich gave a Curvature Index of 2.24 for Femur IV. In forming the Index, however, Weidenreich altered Reid's method (Lageindex I; see Section II.2.iii) and substituted the proximal termination point of the base chord for Reid's distal point. Since no one else has used this method it is not possible to draw comparative data from the literature; Weidenreich observed that "There being, however, an extremely great individual variability of this particular feature, I omitted computing this index on a larger scale for different racial groups". Thus Weidenreich did not think the relative straightness of the shaft of great importance.

Weidenreich was clearly confused about the vertical position of the maximum point or vertex of this curvature. He first stated that "the vertex of the curvature is situated proximally to the midpoint of the shaft" (ibid) and later "the vertex of the curvature is situated below the midpoint of the shaft" (ibid).

Although Weidenreich did not give the position of the vertex it can be calculated from the figures he did give: the base of the curvature = 259 mm.; the distance of the foot of the subtense from the proximal termination point = 67.8% of the base length; therefore, the point of the vertex = 174 mm. from the proximal end of the base chord. This figure, 174 mm., would occur below the midpoint (at 129.5 mm.) of the base chord. Observation of the cast of Femur IV confirms that the vertex of the shaft curvature does occur in the lower shaft.

3. "The bone is flat in the subtrochanteric ... region (hyperplatymeria)" (ibid). Although Femur I and IV are demonstrably flat in the anteroposterior direction in the upper shaft Weidenreich's comparative data on the Platymeric Indices of various hominids and anthropoids is of questionable value. In Table VII he compared the Platymeric Indices of various groups and specimens without any regard for the osteometric technique used by the various authors to obtain the measurements. For example, Pearson and Bell (1919) whose sample of 172 anthropoids was included, used Manouvrier's method of obtaining the Platymeric Index; Weidenreich, on the other hand, used Martin's method (see Section II.2.ii)

and the indices, based on measurements taken by two different techniques, are not comparable. The results of the present study show, however, that the Platymeric Indices of Femora I and IV are at the lower end of the range of comparative sample. Further features of the proximal shaft which Weidenreich considered to be distinctive, the medial and lateral crests and the medial convexity in the subtrochanteric area, are, according to him, associated with the platymeria.

4. "The bone is flat in the ... popliteal region" (ibid); elsewhere, however, he stated "Regarding the distal end of the shaft ... the Sinanthropus femur does not deviate perceptibly from that of modern man. Since, however, only one Sinanthropus femur (Femur IV) is available in which this end is reasonably well preserved, it is difficult to draw general conclusions on the form"

In comparisons of the Popliteal Index, Weidenreich's data must again be questioned. His Table IX includes figures taken from a wide range of publications by authors who used several osteometric techniques in obtaining the lower shaft diameters. Klaatsch (1900) for example, took his measurements at 2 cm. above the distal articular surface while Pearson and Bell (1919) and Manouvrier (1895) took theirs at 4 cm. (See also Section II.2.ii).

With regard to the conformation of the popliteal surface, Weidenreich stated that the plane of this surface in Femur IV is flat and that Dubois' assessment of this feature in the Trinil femora was "gratuitous". Weidenreich pointed out that Manouvrier had found convex popliteal surfaces in his comparative sample, and Weidenreich reproduced sections of the distal shaft of several femora showing the large amount of diversity present.

5. "The bone ... possesses, if any, only a low pilastre" (ibid); but "Femora III and VII possess a pilastre, the latter a remarkably well developed one, while Femora I, II, IV, V and VI have none" while "A slight tendency toward formation of a pilastre is recognizable in Femora IV and V". Thus Weidenreich's observations are somewhat inconsistent; although pilaster formation has been measured by other workers (Pearson and Bell, 1919; Hrdlicka, 1934c) Weidenreich neglected to do this. The Pilastric Index, however, is a reasonably reliable indication of the degree of pilastric formation; In Table VI, Weidenreich gave these values for "Sinanthropus":

Femur I	91.2
Femur II	86.4
Femur IV	85.4
Femur V	79.4
Femur VI	89.3
Average	86.34

Thus, although one cannot be sure that the measurements were taken at the mid-shaft point, it is apparent that the mean of 86. is below Pearson and Bell's mean of 109. for the Pilastric Index and his argument that the shaft is flat both in the subtrochanteric and mid shaft levels can be demonstrated to be true.

The remaining chracteristics of the Chou-kou-tien femora "modern man apparently does not possess" (ibid). Of these, the absence of the lineae pectinae and intertrochanterica, extension of the hypotrochanteric crest to the base of the greater trochanter with a "special tubercle" at the termination of this crest, can be verified on Femora I and IV. Yet Weidenreich stated elsewhere "the proximal end of the Sinanthropus femur ... does not reveal any essential difference from that of modern man (ibid). Moreover it has been shown by Lovejoy and Heiple (1972) that the linea intertrochanterica is a feature of considerable variability in at least one sapient population, and in the present study the proximal continuance of the linea aspera was found in 45.5% of the control specimens.

In his discussion of another of these "distinctive" features, Weidenreich again shows some confusion. He first noted that "the location of the least breadth

of the shaft ... seems (s) to be specific of the *"Sinanthropus"* femur ... In modern man, the constriction usually occurs at, or fairly near, the midpoint of the shaft, whereas in *"Sinanthropus"* it is located far more distally, approximately at the border between the third and the distal quarter of the shaft" (ibid.). Yet in his summary he noted "the proximal position of the least breadth" (Ibid.). It might be conceded that this merely represents a proof-reading error; however, the number of inconsistencies and inaccuracies constitute a serious fault in the monograph.

Another distinctive feature of the *"Sinanthropus"* femur was said to be the relative diameters of the shaft cortex and medullary cavity: "The medullary canal of the shaft is very narrow and the walls correspondingly thick, the former occupying only one-third of the least shaft diameter, whereas the ratio in modern man is one-half" (ibid.). Reference to Table XIV which gives the "Index of Robusticity of the Femur Wall" shows two important mathematical errors.

	Trans. Diam. of the Canal	Index of the Sag. Diam.
Femur I	9.7	37.5
II	6.6	29.9
IV	11.1	40.3
V	8.7	31.7
VI	10.4	38.4
TOTAL	46.5	177.8
Weidenreich's Average	8.13	37.6
Actual Average	9.30	35.56

These figures must not be weighed too heavily since they were merely taken at the line of breakage and do not represent values for the same osteometric point. Nevertheless, the transverse diameter of the medullary canal has a mean value of 1.17 mm. larger than Weidenreich stated and a sagittal index 2.1 points lower. Weidenreich concluded that "this ratio greatly deviates from that of modern man" - a rather sweeping statement since his total comparative sample for this parameter consisted of fourteen specimens.

The last of Weidenreich's "distinctive" features concerns the intrinsic structure of the proximal portion of the femur; "the trajectorial system of the upper epiphysis is far less differentiated and the cancellous tissue much more diffuse" (ibid). Furthermore, Ward's Triangle "is altogether absent in "Sinanthropus" in whom there is a continuous radiation of lamellae over the whole area. The "special pattern of the trajectorial systems" was said to be shared with Neandertal (ibid).

The Ward's triangle area would of course be visible only on Femur IV and it is arguable that

the area is even preserved on that specimen, Weidenreich's x-ray of Femur IV (Plate XXI) shows that the cortical tissue of the inferior surface of the neck is preserved but very little, if any of the lamellar tissue is seen. Moreover, recent x-rays of the Neandertal femora clearly show the presence of Ward's triangle (See Plate I).

In sum then, while it may be argued that the "Sinanthropus" femora show a more or less distinctive morphological pattern, this pattern is not necessarily distinctive of all the component populations at this particular grade of hominid organisation.

The conspecificity of the Chinese and Javan specimens has not been seriously challenged since the mid-1940's and most authors (Dobzhansky, 1944; Mayr, 1945, 1950; Le Gros Clark, 1955) refer the specimens to *Homo erectus* without question.

With the discovery of new material possibly referrable to *Homo erectus* and the realization that some known specimens might belong to that taxon, Campbell suggested that the taxonomy of the Middle Pleistocene hominids should be revised. His first revision (1963) included the sub-species *pekinensis* and *erectus* within *Homo erectus*. In 1965, Campbell

added a further six sub-species: *leakyi*, *heidelbergensis*, *habilis*, *mauritanicus*, *modjokertensis* and *capensis*. This revision has been accepted by Howells (1966) who added H.e. *lantiensis* and *H.e. soloensis*.

By 1930, ten depositional levels were recognised at Locality I and the overall temporal and faunal homogeneity of the deposits was emphasized. In particular, *Hyaena* sp. was said to be the same throughout the levels and a "Pre-loessic lower Pleistocene" age was suggested (Chardin and Young, 1930). (The loess is of upper Pleistocene age). By 1933, three main cultural phases were recognized in a total of eleven stratigraphic layers. The faunal assemblage showed many affinities with the Sanmenian (Late Pliocene) although the inclusion of more advanced forms suggested a lower Pleistocene date (Black et al. 1933). In early reports the levels from which the non-hominid faunal remains had been recovered were reported in a somewhat incidental and imprecise fashion.

Three areas within the Locality I site were recognized in 1933:

1. The main deposit - the central and largest part of the deposit.

2. The lower fissure, the "pediculate" part of the deposit approximately 7 m. wide and extending north from the main deposit; this area was worked intensively during 1928-1930.

3. The Kotzetang Cave, an artifical cave formed during quarrying in the eastern part of the deposits.

At this time, the main deposit and lower fissure were recognized to contain the following layers.

Layers 1-2: upper breccia and upper travertine including a stalagmitic soil (4.5 m).

Layer 3: collapsed roof of irregular breccia (3m.)

Layer 4: upper ashy layer, with a thick accumulation of thickly laminated clays. Much charcoal debris and stone artifacts. Burnt *Euryceros* and *Elephas* remains are present but rare (5.5 m).

Layer 5: thin, partly brecciated black clay probably representing the base of Layer 4 (0.4 m).

Layers 4 and 5 contain Cultural Zone A. This archaeological assemblage shows "a distinct advance both in the selection of material used and in the shape of artifacts" (Black et al, 1933/133). There are more "bipolar flakes" and an increased utilization of flinty material than in the lower layers.

Layer 6: fossiliferous hard breccia forming, in part, a consolidated stalagmitic floor (8 m.)

Layer 7: sandy layer with well preserved *Sus* and *Bubalus*, often showing carnivore (and human?) tooth marks. (6.5m)

Layer 8-9: "carnivore layer" in irregular breccia, including *Hyaena, Ursus, Trogontherium, Hystrix* and *Arctomys* (6.5m).

Between layers 9 and 10: ashy layer, probably corresponding to Cultural Zone C (vide infra.).

Layer 10: lower travertine with some breccia ending below in red, sandy clay. The deepest levels show evidence of abrasion in an underground stream. These levels in the lower, eastern portion contain *"Sinanthropus"* and *Rhinoceros mercki*. Cultural Zone C is found in these levels in association with *Hyaena sinensis, Equus sanmeniensis, Eryceros pachyosteus* and *Elephas namadicus*.

This cultural zone was excavated over an area of 160 sq. m. the tools are mostly in green sandstone but also in vein quartz. Thousands of broken stones were found in these layers but probably only about 150 chipped tools (ibid); they include flaked choppers, quartz cores, scrapers and "burin-type" tools. (12 m.+).

Cultural Zone B was found only in two thin layers (50 cm.) in the Kotzetang Cave region; it was 8 m. below Cultural Zone A and 4 m. above Cultural Zone C. It is comprised of a very small series of flaked choppers very similar to those in Cultural Zone C (ibid).

Approximately 75 "scratched and incised bones" were found throughout the deposit; on some of these"human workmanship (is) clearly impressed" (Black et al, 1933).

Movius (1944) in a re-evaluation of the stratigraphic evidence mentioned "over a dozen individual strata" with three main stages: upper travertine, main cultural horizon with hearths and banded clays, and the lower breccia. In his opinion, the absence of *Hipparion* and *Chalicotherium* suggest a date later than the Villefranchian and although he is reluctant to equate the deposits with the European glacial sequence he nevertheless suggests a date contemporary with the 2nd interglacial (Holsteinian). He, too, stresses the faunal and depositional homogeneity of the deposits and states that they must have been laid down in a single depositional cycle. He also STRESSES that the faunal and depositional homogeneity of the deposits and states that they must have been laid down in a single depositional cycle. He also states that the fauna at Locality 13, 1 km. south of

Locality I, differs from a usual Middle Pleistocene sequence in having *Hystrix lagarelli* and *Euryceros flabellatus*; it therefore probably dates to the 2nd Himalayan glaciation. Locality 15 probably dates to the 3rd Himalayan glaciation (ibid).

Further attempts to date Locality I on the basis of the faunal remains were undertaken in the late fifties (Kurten 1957 a, b). Kahlke and Hu (1957) suggested that *Megaceros giganteus antecedens* from the Steinheim site is very like the *Megaceros* sp. found at Locality I. The Steinheim site is dated to the Holsteinian and they suggest a similar date for Locality I. A similar suggestion is made by Kahlke and Chow (1961). Kurten has attempted to use the replacement of *Hyaena brevirostris* by *Crocuta crocuta* as a temporal marker with widespread application (1957 a, b). He states: "The first appearance of *Crocuta crocuta* in any stratigraphic column is therefore an event which, in principle, can be correlated with absolute precision ... on this basis, all faunas with *C. crocuta* may be dated as late Cromerian or later; all faunas with *H. brevirostris* as the Villefranchian or Cromerian; and all faunas with both as late Cromerian" (1957a). Although he neglected to mention at which level in Locality I this replacement took place he dates this site (and the Australopithecine site at Swartkrans) as Late Cromerian (ibid).

The Cromerian date was severely criticised by Kahlke and Chow (1961) and Kurten later revised his estimated date on the basis of a pollen analysis of matrix taken from a specimen of *Megaceros pachyosteus* from Locality I; the level from which the *Magaceros* specimen was derived was not given (Kurten, 1959, 1960: Kurten and Vasari, 1960). The pollen grains totalled 132; 9 spores were also recovered. The pollen spectrum was "surprisingly similar" to that from a northern coniferous forest (Kurten and Vasari, 1960) and was suggestive of relatively cool conditions. It further suggested nearby steppe conditions but with pine and spruce on the hills. Occupation at Locality I, it was agreed, probably occurred during a European glacial and not in an interglacial; Mindel II is suggested (Kurten 1959, 1960). As this stadial has a potassium/argon date of 360,000 BP for Europe (Everden, Curtis and Kistler, 1958) Kurten also suggests this date for Locality I (1959).

Chaney (1935) also suggested cool, dry conditions during the occupation of Locality I on the basis of the occurrence of endocarps of *Celtis barbouri* (hackberries). This species does not itself require such climatic conditions but the absence of stem and leaf remains in the deposits was suggestive of a "climate so arid as to prevent their entrance into the sedimentary record" (ibid).

When excavations were resumed in 1958 by the Institute of Vertebrate Palaeontology of the Academia Sinica it became clear that the Locality I deposits were not as homogenous temporally, stratigraphically or faunally as was previously thought. In the course of 1958 season thirteen levels were recognized and these were subsequently divided into three major groups (Chia, 1959).

Layers 1-3, Group C: Layers 1 and 2 of yellowish loam or breccia, including a layer of travertine; layer 3 of reddish breccia. Group C was given a date of Late Middle Pleistocene on depositional correlations with Locality 15 whose "lithological characters are exactly the same as these levels in Locality I", (ibid).

Layers 4-10, Group B: Breccia and 3 layers of ash with homogeneous fauna and artifacts; layer 5 contains travertine and layers 8 and 9 have an abundance of scrapers and choppers, mostly made from green sandstone. There is a decrease in the number of tools from layer 6 upwards; tool specimens from layer 4, often in vein quartz, are regularly shaped unifaces of long, thin shape and were probably detached from a prepared core.

Layers 11-13, Group A: sand, conglomerates and red clay; very few fossils, a single stone tool and no

sign of ash. The single tool is a flake detached from a chert pebble. The bottom of the fossiliferous deposits was apparently reached in excavations near the northern wall. The occurrence of *Euryceros flabellatus* in Group A, a "typically early Middle Pleistocene form" would seem to date these lower levels to that time; this species also occurs at Locality 13 and Chia suggested that this locality was contemporaneous with the lowest levels at Locality I.

Chia suggested that the two layers of travertine indicate interruptions in the process of deposition. A further interruption may have occurred in layer 12 where a large lens of red sand is encountered (ibid).

Huang (1960) recognized 6 depositional levels correlated with four temporal categories within the Pleistocene. The basis for these dates is "geological" but precise reasons are not stated.

I: Early Pleistocene; basal gravels with red clay and coarse sand,

II: Early Middle Pleistocene; lower and middle breccia,

IV and V: Middle Pleistocene; sand and breccia with ash and stalagmitic deposits,

VI: Late Pleistocene: upper breccia.

Kahlke and Chow (1961), like Chia, record 13 depositional layers which they divide into 8 sections on the basis of faunal assemblages. They point out the difficulty of describing these faunal groups since earlier workers did not always record the level of their finds and the precise layer by layer faunal analyses have not yet been made. This new faunal information, still very incomplete, has been compiled since the digging resumed in 1958. Layers 11-5 present a faunal assemblage very similar in some respects with deposits of Holsteinian age in Europe; *Trogontherium cuvieri* and *Ursus spelaeus* have apparently exact counterparts at the Swanscombe site. The specialised *Megaceros* sp. and *Machairodus inexpectatus* had their counterparts at the Steinheim site, also of Holsteinian age. These levels (11-5) also contain *Hyaena brevirostris* which is replaced by *Crocuta ultima* in levels 1-3. In summary, they concluded that the Locality I faunal assemblage has a close similarity with the South-East Asian *Stegodon/Ailuropoda* fauna and suggest a temperate, second inter-glacial occupation. This suggestion is supported by Oakley (1964).

Hsu (1966) undertook a palaeobotanical investigation of Locality I involving the extraction of pollen at 1 m. intervals from 9.3 m. to 33 m. below the top of the deposits; below 33m. samples were taken at 20 cm. intervals

It was not possible to obtain samples above 9.3 m. A total of 27 samples yielded 1897 pollen and spores. Hsu recognized 3 botanical assemblages which gave quite different sporo-pollen spectra. He suggests that these "almost correspond" to the 3 cycles of deposition represented by the basal gravel, middle breccia and the upper loam, sand and breccia group.

Stage I: 40 m. to 36 m. (basal gravel); pollen representing *Cupressaceae* (c.f. Juniperus) and several members of Compositae including *Artemisia* and *Chenopoiaceae*. Spores of Bryophytes and *Botrychium* are abundant. This last genus grows, today, only in altitudes above 2500 m. and is often associated with lichen and mosses; this spectrum is strongly representative of a cold climate.

Stage II: 36 m. to 20.5 m (Middle breccia); low in the sequence, pollen of *Abies* and *Betula* suggest a cold, temperate zone. Immediately above, *Pinus*, *Quercus*, *Pistacea*, *Alnus* and *Salix* suggest a mixed forest and warm, temperate climate. Toward the end of this sequence *Betula* markedly decreases and the appearance of *Symplocis* suggests an increase in the temperature.

Stage III: 20.5 m. to 9.3 m. (upper group); a continuation of the warm-living genera: *Carpinus*, *Corylus* and *Symplocis*. Toward the end of this sequence *Betula* again increases and this suggests an increasing coolness.

Hsu suggests only "an interglacial" period for occupation at Locality I (ibid).

The most surprising single feature about these early attempts to date Locality I is the assumption that the deposits, more than 50 m. deep, were homogeneous and contemporaneous Nowhere is this assumption seen more clearly than in the work of Kurten. In his numerous studies of the Locality I fauna he never mentions the level from which his material was derived. This failure makes his work with the *Hyaena/Crocuta* replacement valueless in this instance. Moreover, it is hazardous to attempt precise dating through negative faunal evidence since a large number of factors influence the local occurrence and fossilization of organisms. Later work has suggested that the cave deposits were accumulated over a considerable period of time, a time perhaps not totally containable within a single Pleistocene phase.

Surprising, too, is how the significance of the stalagmitic travertine layers escaped virtually all the earlier workers. Chia's interpretation of these, as an interruption in the depositional process, seems reasonable.

Hsu's botanical investigation finds considerable support in the palaeontological assessment of Kahlke and Chow. A cold climate during the deposition of the basal gravels seems acceptable on the basis of the lithology cold spectrum flora

and by the occurrence of *Ursos arctos*. The Holsteinian date of the Middle Breccias is strongly suggested from all available evidence. The close relationship, if not specific identity, of many of the large mammals with European forms thought to be Holsteinian, is also supportive of this date.

Excavations continued in 1959 and 1960 (Chia, 1959; Woo and Chao, 1959: Chao, 1960); Hsu (1966) does not record the dates of his field work. Reports of subsequent investigations at Locality I have not been received in the West.

It has not yet been possible to attempt absolute dating of the deposits.

II.3.ii - Java:

In 1890 Dubois began collecting vertebrate specimens at two sites in central Java: in the Kendeng Hills and at Trinil. The latter site is on the left bank of a meander of the Solo (Bengawan) River, opposite the village of Trinil. These sites had been known for some time to both native and Dutch collectors (de Terra, 1943). In 1890 Dubois recovered a fragmentary mandible at Kedung Brubus and in September, 1891 he found a molar at Trinil which he attributed to a new genus *Anthropopithecus* an early Chimpanzee (Dubois 1891a)[1]. The calotte was found one month later and was allocated to the same genus (Dubois 1891b). Femur I was discovered in August 1892 approximately 15 m. from the site of the calotte and in the same level; Dubois considered this to be from the same individual as the *Anthropopithecus* calotte (Dubois 1893). Two more teeth were later found at this site: a molar, in October 1892 and a premolar in 1896 (De Terra, 1943).

In 1894 Dubois altered his first opinion of the Trinil specimens and proposed a new family, Pithecanthropidae, intermediate between the Simiidae and the Hominidae to contain the material. This family was defined as follows:

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[1] Dubois' early papers (1891a, b; 1893 and 1894) are not available in England. This discussion was derived from Turner, 1895; Hrdlicka, 1930, de Terra, 1943 and Boule and Vallois 1957.

> "Brain case, absolutely and in relation to the size of the body much more spacious than in Simiidae, but less spacious then in the Hominidae: contents of the cranial cavity about two-thirds of the average contents of that of man; the slope forward of the occipital bone below the protuberance and superior curved line much stronger than in the Simiidae. Teeth, although retrogressing, yet of the type of the Simiidae. Femur, in its dimensions, like the human, and constructed for progression in the erect atitute"
>
> (Dubois 1894, quoted from Turner 1895).

Within this family, the taxon *Pithecanthropus erectus* was suggested for the Trinil specimens. This nomen had earlier been proposed by Haeckel for the "missing link" and was the (theoretical) precursor of *"Homo stupidus"* (Haeckel, 1889).

In 1895 Manouvrier published two papers dealing with the *Pithecanthropus erectus* material from Java (1895 a, b). In the first paper he described the femur as being "humaine" but was not certain of the association between the calotte, femur and molars. Although he stated that the morphology of the two molars was similar to that found among the "Neo-Caldeonians" he concluded that Dubois' attribution of these specimens to a large gibbon[1] was acceptable. On October 31

[1] There is some confusion in the literature as to just what sort of Primate *Anthropopithecus* really was. Manouvrier clearly was discussing a "hylobatid" and Dubois' recognition of "hylobatid" characters in the Trinil material is in evidence at least as early as 1896. Nevertheless, de Terra in discussing *Anthropopithecus* refers to is asa Chimpanzee and the word is placed in quotation marks (1943).

1895, Manouvrier was able to view the original Trinil material in Paris; he stated that this examination "a produit sur moi une impression trés differente de celle produit par la vue des dessins, photogravures et par les descriptions" (1895). He was primarily struck by the degree of fossilisation of the material which "disparaitre les doutes ... de leur ancienneté et de leur contemporaneité". This lead him to argue against "le hazard" bringing together in one small area representatives of 2 or 3 different species and he suggested that it was much more likely that the teeth, calotte and femur belonged to the same individual. In describing the osteophytic lesion on the Trinil femur Manouvrier recalled that Virchow had found similar lesions on the femora of two individuals who also had vertebral "abces"; Manouvrier then concluded that "Sa function de locomotion fut serieusement geneé par la lesion vertebral, par la lesion femorale, par les troubles generaux consecutifs et peut-être aussi anterieurs a ces deux lesions". He further argued that some of the morphological features suggested by Dubois to be of taxonomic significance were actually due to this pathology. Among those features were the straightness of the shaft and the roundness of the popliteal area. The large apophysis on the proximal portion of the external condyle, however, possibly reflected "une disposition musculaire normale dans cette espece". Manouvrier concluded that the combination of small cranial capacity and bipedal locomotion indicated that the "missing link" had been found and that Dubois' discovery should stand as an affirmation of

the theory of evolution.

Dubois (1896) discussed the stratigraphy of the Solo River site at Trinil and pointed out that the bone-bed showed an east-west dip of from 3° to 15° and was probably "young Pliocene" in date; he later (1908) reaffirmed his belief in a Pliocene date[1] for the Trinil fauna. In 1896 he again emphasised the "transitional nature of the Trinil material and stated that certain features of the femur were not found to such a degree nor found together in man, although they were said to occur in *Hylobates*. These features are:

1. roundness of the inner side of the shaft
2. convexity of the popliteal surface
3. small development of the trochanteric line
4. shortness of the spiral line (possibly related to the exostosis).

Manouvrier (1896) responded to Dubois' paper by reaffirming his suggestion of the essentially human, although primitive, nature of the Trinil material; to support this position Manouvrier proposed the nomen *"Homo pithecanthropus"* for the specimens.

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[1] It should be pointed out that the Plio/Pleistocene boundary is still the subject of some controversy.

Houze' (1896) responded by suggesting the nomen "*Homo javanensis primigenius*" and Alsberg (1922) suggested "*Homo trinilis*".

Turner (1895, 1896) disagreed with Dubois' suggestion that certain features of the Trinil femur were outside the normal human range; he stated that if Dubois' comparative sample had been larger he would have discovered that the characteristics were within the normal human range. He further suggested that it was "extremely doubtful" that the calotte and femur belonged to the same individual. Turner, however, was in error in stating that the fossils were "lying in an alluvium brought down in the course of a tropical river" (1895) but correctly noted that while the features, including the exostosis of the femur are sharp and unworn the calotte does show signs of post mortem abrasion. Turner finally suggested (1896) that the convexity of the popliteal surface may have been due to a localized increase in periosteal activity related to the pathology; he utterly rejected the possibility that the femur was that of a gibbon.

Virchow, who reportedly "never tired of attacking the hated ape theory" (Haeckel, 1906) emphatically denied that "*Pithecanthropus*" was in any way related to man (1896). He concurred with Dubois' opinion that the straightness of the shaft was a hylobatid feature

and suggested that the specimens might belong to a "gigantic" form of that animal.

Hepburn (1897a) agreed with Manouvrier (1895b, 1896) but disagreed with Dubois (1896) regarding the distinctiveness of the Trinil femur. Hepburn was able to find convex popliteal surfaces, convexity of the anterior intertrochanteric line and convexity of the medial shaft both separately and together in the femora of living groups. He concluded that the "frequency with which these features are found on the human femora entitles them to rank as human characteristics" ; he suggested that the Trinil femur should be attributed to the genus *Homo*.

Bumuller (1899) basing his argument on Dubois' assessment of the "hylobatid" features of the Trinil material proposed a new species "*Hylobates giganteus*" to include the specimens. He argued that a ratio revealed in the "Bandradienindex" of the lower end of the Trinil femur was closer to an ape than to man. This index describes tha articular curve of the lateral condyle through the distance of the mid point of the tuberosity of the fibular lateral ligament to the posterior and distal extents of the condyle.

Krause (1909) accepted Bumuller's generic attribution but suggested the specific nomen '*Homo giga*s. Boule

(1921, 1923) concurred that the Trinil material was from a gibbon or a closely related group.

Wilser (1900) could not agree that the Javan material showed fully human features and allocated it to *"Proanthropus"*

Morselli (1901) accepted the specimens as an early type of man and suggested they be contained within *"Pithecanthropus duboisii."*.

The Trinil site was further investigated by Dubois' team between 1898 and 1901 and in 1906 an expedition lead by Frau Selenka arrived to continue the work (Selenka and Blanckenhorn, 1911). During the ensuing field season the site where the calotte had been found was excavated to a depth of 40' removing, in the process, approximately $10,000^3$ yards of soil (De Terra, 1943). No further hominids were found at Trinil but the "Sonde tooth" was recovered at about 4 miles upstream (ibid.).

Carthaus, a geologist with the expedition, made the first detailed investigation of the site. He reported that the bone bed from which the *'Pithecanthropus'* material had been obtained, consisted of tuffs, pumice and andesite and a few clay lenses and was 40 cm. to 1 m. thick. He viewed the very rich bone bed as having been accumulated in an explosive episode during a volcanic eruption. Yet,

although the bones in the deposit showed no evidence of water transport few of the bones were complete and none were articulated. He attributed this to a lahar stream passing over an area previously "ravished" by volcanic eruptions and which was littered with carcasses. Carthaus concluded that the fauna in the bone bed was contemporaneous with the period of deposition and on the basis of the presence of *Stegodon trigonocephalus* was of Middle Pleistocene age, (Selenka and Blanckenhorn, 1911). Stremme and Janenshe, reporting in the same volume, however, concluded that it was not possible to evaluate the age of the deposit since it did not include enough index fossils.

Dubois (1926a) while acknowledging the close resemblance between the Trinil femur and that of man, nevertheless pointed out two features which "distinguish (it) very decidedly from that of man". The first of these features was the convex popliteal surface which formed, in Dubois' discussion, a median buttress and indicated that body weight, which is transferred mainly through the lateral condyle in man, must have been transferred more medially in *'Pithecanthropus'*. Moreover, the absence of the angulus medialis indicated that vastus intermedius and medialis muscles may have had an origin more similar to that found in the apes. Dubois also asserted that the portio pubica of adductor magnus had a "fleshy median attachment" similar to the condition which occurs in the "Monkey Tribe"; this form of insertion could indicate that adductor magnus acted as an outward rotator as well as an abductor.

The second distinguishing feature of the Trinil femur was said to be the verticality of the posterior border of the greater trochanter. In man and most other Primates except *Hylobates* this border runs obliquely forward. This suggested a "peculiar action" of gluteus medius and minimus muscles; thus the tendon of gluteus medius, being inserted behind the axis of rotation of the hip joint was in a position to act as a strong outward rotator as well as an abductor. Therefore, in a position with the leg fixed the small glutei could act to rotate the trunk. The total locomotor pattern was one, then, where the weight was borne on the inner border of the foot; such lomomotion, Dubois suggested, could be beneficial when climbing trees.

In the same year Dubois (1926b) published radiographs of the upper and lower portions of the Trinil femur. He pointed out that the "static trajectorium" as defined by Walkhoff and the "zug trajectorium" as defined by Wolff, were both present and intersected at right angles. He suggested, therefore, that the mesh and lamellar structures resembled those found in man and differed from the condition in the anthropoids.

In 1932 Dubois reiterated his conclusions as to the "human-ness" of the Trinil specimens and described three further femora in the Leiden Museum which had come from Java. These femora *'Pithecanthropus' II, III, and IV*

were suggested to have come from the same group as *'Pithecanthropus" I* and Dubois described the points of similarity between all of these specimens. In particular, he noted the rounding of the lower shaft and the convex popliteal surface, the "continued labium laterale cristae femoris" and the perpendicular posterior border of the greater trochanter in Femora I and II. He again described functional differences in adductor magnus and gluteus medius and minimus and now proposed the term "dendrobates" to describe the particular type of climbing activity associated with this morphology.

In 1934 Dubois reported the discovery of a further femur (*Pithecanthropus" V*) at the Leiden Museum. Because of corrosion, which had removed the external cortex from the specimen, it became possible to compare the outer surface of this bone with *'Pithecanthropus' III and IV* which had been similarily affected after burial. In femora III and IV "the structure of the periosteal bone layer is a perpendicular one, i.e. the osteones, with the Haversian canals, have a general direction about parallel with the axis of the shaft of the femur. The internal bone structure ... of specimen V is different. Here the Haversian canals, and consequently the axes of the osteones have oblique directions forming angles with the axis of the shaft of from 10 degrees to 20 degrees (Dubois, 1934). This difference, once stated, was never mentioned again

and all emphasis was laid on the oblique osteon structure of Femur V. Dubois correlated the orientation of the osteones with the direction of the action of vastus medialis and lateralis. In his conclusions regarding the osteon arrangement of Femur V, Dubois more firmly established the basis for his remarkable *volte face* in the following year regarding the taxonomic position of "*Pithecanthropus*." Dubois used the evidence of the different osteon arrangement to support his previously stated idea (1926a, 1932) that the vasti acted differently in "*Pithecanthropus*" than in modern man; there must have been "easier and habitual rotation in the knee joint" and the "vasti muscles were strongly active to stiffen the knee joint in every stage of flexion". Thus "In all probability the described incessant muscular effort was necessary in the erect gait of '*Pithecanthropus*' for the habitual use of the leg on uneven ground or on trees, yet with frequent assistance of the hand".

Later, Dubois (1935a) disclosed the discovery of yet another Javan femur in the Leiden Museum; this apparently had not come from the Solo River site at Trinil but was possibly found at Kedung Brubus. Dubois was at first reluctant to attribute this specimen to '*Pithecanthropus*' because of the placement of the crista on the shaft resulting in a cross section "different from the other ones".

Nevertheless, after cleaning and preparation of the specimen Dubois was convinced that it was from *'Pithecanthropus'* and the "inward shifting of the crista femoris ... (should) be regarded as an individual variety". Corrosion had again removed much of the outer cortex and "a diagonal system of structural stripes" was revealed similar to Femur V.

Dubois (1935a) now reversed his previous opinion about the hominine nature of the Javan material and, at this time, described *'Pithecanthropus'* as a "gibbon-like creature". His reasoning is somewhat tortuous but his argument relies mainly on the structure of the brain, as discerned from the calotte, and his long-held though rather equivocal ideas regarding several "hylobatid" features of the femora. Thus, the precursors of this remarkable turn of mind had occurred in earlier papers (1896, 1926a). To support this new attribution Dubois proposed a "Law of the Autonomic Phylogenetic Progression of the Psychencephalon" which relied on values for "K" derived from the formula:

$$K = \frac{E}{S}\ 5/9$$

Where: K = coefficient of cephalization

E = weight of the brain

S = weight of the body.

Dubois thus suggested a direct relationship between body weight, brain weight and the degree of development of the cerebral hemispheres. He stated that there would be

a geometric progression for values of "K" throughout the Mammalia with only a single gap -- between the "anthropomorphous" apes and man. This void was to be filled by *'Pithecanthropus'*. This idea has more recently been revived by Le Gallic (1956).

Dubois derived his estimate of the body weight of *'Pithecanthropus'* by the formula:

$$\text{Weight} = \text{length of the mechanical axis} \times \text{smallest diameter of the femur}^2 = 104 \text{ kg.}$$

Dubois then assumed that "an immaginary (sic) giant Siamang possessing a femur twice as long and twice as thick as areal Siamang would have weighed eight times as much, assuming the same bodily proportions. Now the relative weights calculated from a comparison of the *'Pithecanthropus'* femur with that of our quite full grown and large male siamang are as 8.083:1 and

$$\frac{104}{8.083} = 12.866 \text{ kg.}$$

This calculated weight is almost exactly the weight observed in such a large siamang" (ibid. p. 582). He further concluded that because the weight was thus "verified" *'Pithecanthropus'* had body proportions similar to the Siamang and Gibbon and that the "upper limbs still exerted locomotive functions, at least habitually, in a similar manner as in the Gibbons" (ibid.).

Dubois reiterated these conclusions in a paper two years

later (1937a). In this paper he again reasserted the distinctiveness of the osteon structure of Femur V which was said to be "entirely different from the human one". Dubois developed this argument in a paper published later that same year (1937b). Here, he compared the osteon arrangement of Femur V with the arrangement on seven plague pit femora from Leiden. In view of the intricately wrought argument he had developed to support his allocation of *Pithecanthropus* to a gibbon-like group his conclusion here is surprising. "... it appeared that on all of them (the seven Leiden femora) the osteon arrangement is identical with that of the fossil '*Pithecanthropus*' Femur V... Of course the now found structural and functional similarity of Man and '*Pithecanthropus*' is new evidence of relationship between the two. Not, however, of organismal identity ... for the distinctness of '*Pithecanthropus*' is firmly established by certain constant external characters of the thigh bone, and, above all, by that determinant character, the cephalization level, which in '*Pithecanthropus*' is one degree below that in Man. An analogous case we meet with in '*Australopithecus transvaalensis*' ; its cephalization level, however, compels to place this species with Anthropoid apes" (ibid.).

In his last paper, published two years before his death, Dubois (1938) maintained his view that '*Pithecanthropus*'

was a gibbon, but the opinion was stated in a much softened and ameliorated form. Moreover, he maintained that the femora of '*Sinanthropus*' showed "essential differences" from those of the Javan specimens.

Dubois' attribution was largely ignored although as late as 1957 Boule and Vallois suggested his hypothesis as a possible interpretation of the material. Boule and Vallois' acceptance of Dubois' view on the Trinil femora may have been influenced, in a degree, by a mistranslation of the word "osteon" to mean "trabeculation": i.e. "A special direction of the bony trabeculae has been disclosed"(ibid.). Dubois discussed a different orientation of the osteones in Femur V but never made such a statement with regard to trabecular patterns.

By the late 1930's many workers had remarked on the similarities between the Chinese and Javan crania although several had noted differences in the femora of the two groups[1].

Although Weidenreich acknowledged a close phylogenetic relationship between the Chinese and Javan crania he emphatically stated that none of the four Trinil femora (I,II,III and IV) "belong to *Pithecanthropus* but must be attributed to a type more closely related to modern man" (1941). Moreover, "The differences between the

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1. A discussion of these arguments can be found in Section II.2.i.

Sinanthropus and Trinil femora are too substantial to be explained as mere individual or racial variations" (ibid.). He was, therefore, skeptical regarding the provenance of Dubois' "new femora" and pointed out, as von Koenigswald did later (1968) that a label on a box was no proof that the bones belonged to '*Pithecanthropus*.'

Weidenreich's refusal to accept the questionable provenance of the femora displayed appropriate caution but his tenacious grasp on the narrow limits of typological classification was somewhat less rational. His arguments on why femoral specimens from the two sites should be separated revealed that he had failed to recognize that fossil populations must have comprised, just as living populations do, polytypic species with considerable ranges of variation. Moreover, as Mayr (1963) has pointed out, different populations of polytypic species may evolve at differential rates and during the periods of Java's isolation conditions would have enhanced intra-specific variability. Weidenreich, however, is not the only worker to maintain a typological approach to hominid taxonomy long after the ethos of typology has been shown to be inapplicable in classificatory problems.

Von Koenigswald began investigating the geology of Java in the early 1930's and, working with the index

fossil technique, recognized three consecutive Pleistocene faunas : the Djetis, the Trinil and the Ngandong. The Trinil fauna is derived from the Kaboeh deposits which overlie the Poetjangan layers containing the Djetis fauna (von Koenigswald, 1950). Although the dating of the Djetis fauna is still open to some dispute (see especially Hooijer, 1951), the Trinil fauna is widely regarded as Middle Pleistocene in date (de Terra, 1943 : von Koenigswald, 1950; Hooijer, 1951). Following the conclusions of Schuster (in Selenka and Blanckenhorn, 1911) de Terra has argued that the bone layer at Trinil was deposited during a time of increased cold, possibly equivalent to a glacial episode in the northern Himalayas. His argument was based mainly on the existence, in the bone bed, of certain plant remains (notably *Viburnum sp.*, *Reevesia sp*, *Liquidamber sp.* and certain Laurels) which require a prevailing temperature of 6 degrees to 8 degrees lower than that at Trinil today. "This thermal difference corresponds to an altitudinal variation of about 1100 m. and a snowline of about 3000 to 3100 m. The latter computation has a distinct analog to the snowline depression of the Second Interglacial in the Himalayas" (1943).

The major point of the dispute over the Trinil hominids, however, is not the geologic age of the horizon from which the Trinil fauna is derived but the contemporaneity of the

fossil hominids from that horizon both with each other and with the period of original deposition.

Hrdlicka, who visited the Trinil site in 1925, seems to have been the first to suggest that it could be a "secondary deposit, containing a mixture of forms" (1930). De Terra made a similar suggestion:

> "At the time of our visit on the site it occurred to me that two low terraces could be recognized at Trinil... Now since Dubois as well as later investigators dug on that side of the stream meander where deposition is still taking place, is it possible that their pits were partially sunk into this younger terrace? To all appearances these deposits should be post-Pleistocene (and) it is therefore conceivable that some of the fossils excavated were derived from this horizon. Nevertheless, incomplete as the initial excavation records are, it would seem that most of them, especially the *Pithecanthropus* remains, were actually discovered *in situ* in the bone bed" (de Terra, 1943).

Thus, although de Terra recognized that it was possible that the Trinil hominids had been derived from a horizon of other than Middle Pleistocene date he did not think it probable.

An attempt to evaluate the contemporaneity of the Trinil fauna was made by Bergman and Karsten (1952). Using a method of fluorine analysis developed by Oakley they measured the amount of fluorine deposited by ground water in the six Javan femora, the calotte, a crocodile, two bovids and a specimen of *Duboisia*. Their results are given as follows:

	FLUORINE (in %)	
Calotte	1.22	1.20
Femur I, compacta	1.05	1.12
Femur III	1.34	1.43
Femur IV	1.38	1.43
Femur V	1.10	1.02
Femur VI	1.50	1.56
Femur I exostosis	0.75	0.74
Femur II spongiosa	0.064	0.069
Femur III outer layer	0.76	0.67
TRINIL FAUNA		
Duboisia	1.35	1.46
Crocodile	1.48	1.50
Bovid	1.17	1.20
Bovid	1.72	1.75

Although it is obvious from the results on hominid bone that the type of bone chosen for the sample is extremely important, Bergman and Karsten do not record the type of bone taken from the other Trinil vertebrates. It is therefore not possible to be sure that the results are strictly comparable. Nevertheless, they concluded that "there is a very good concordance between the fluorine content of the human remains and that of the animals of the same deposit (and this) is a conclusive argument for settling the dispute about the relative age of those bones" (1951). They went on to state that "Judging by the fluorine content, the skull and the femora of *Pithecanthropus* and of the animal bones from Trinil can be dated in the Middle Pleistocene". This last sentence reveals that Bergman and Karsten misunderstood the Limitations of fluorine analysis in dating problems; it is a useful method for determining the contemporaneity

of specimens derived from a single site but is of no value in determining the absolute age of that material.

Von Koenigswald (1968b) has, however, published an estimate of the date of the Trinil fauna using potassium/argon ratios which may be valid in chronometric determinations. Although material from the Trinil site itself was not analyzed, leucite from volcanic deposits in another part of Java which contained Trinil fauna gave an absolute age of c. 500,000 B.P. A tektite from a site about 20 m. above the base of the Kabuh beds has given a date of 730,000 ± 50,000 B.P. This date, however, reflects the time of the tektite's entry into the atmosphere and does not indicate the time of its inclusion into a particular strata.

Further attempts to assess the contemporaneity of the Trinil femora and calotte have been reported by Day and Molleson (in press). In this investigation, four techniques of relative dating have been used the analysis of the ratios of fluorine and other depositional minerals, measurement of nitrogen levels in bone collagen, radiometric analysis of beta emission rates and optical spectrography. Day and Molleson report that the fluorine/phosphate levels confirm the results of Bergman and Karsten. The beta emission levels were nil and the nitrogen analysis revealed that Femur I had higher

levels than any of the other examined bones. The higher nitrogen level may in fact be due to the fact that Dubois had boiled the specimen in glue. The optical spectrography demonstrated that the calotte and femora shared a number of elements such as aluminium, titanium and chromium; however, this is a non-quantitative method and these results suggest mainly that the specimens were derived from a single site. They concluded that the results are "inconclusive" in determining the contemporaneity of the Trinil hominids but tended to confirm the provenance of the material.

II.3.iii: SOUTH AFRICA: The first formal report of the existence of an early Pleistocene hominid from deposits in South Africa was made by Raymond Dart in 1925; the taxon *Australopithecus africanus* was proposed at this time. Gregory and Hellman (1939) erected a new sub family within the Hominoidea, the Australopithecinae.

The first femoral fragment attributed to this group was reported by Broom and Schepers (1946). This fragment[1] of a distal left femur had been recovered from the lower cave deposits at Sterkfontein in 1937 (Le Gros Clark, 1967). Broom reported that he had taken the Sterkfontein pelvis and femur to New York in 1937 to be examined by Gregory. After many comparisons he decided the specimens belonged to a "giant baboon" possibly *Dinopithecus* (ibid.). However, Broom and Schepers (1946) were clearly convinced of the hominid characters of the Sterkfontein pelvis and femur and attributed it to *Plesianthropus transvaalensis*. This first femoral fragment is described as being "very human" and from "an animal that walked ... entirely or almost entirely on its hind feet". It did, however, show several "peculiarities" in the intercondyloid fossa. The fossa was said to extend more into the anterior surface than was observed in "over 100 Kafirs

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1. Although Broom and Schepers did not include specimen numbers in this monograph, the Catalogue of Fossil Hominids states that TM 1513, a distal left fragment was found in 1936 (Broom and Schepers state 1937); it seems safe to assume this is TM 1513.

Europeans and Australians". A second femoral fragment was also mentioned in the 1946 monograph:

> "It seems unwise to describe this badly crushed femur in detail as the California University Expedition has found the beautifully preserved upper third of a femur apparently of an Australopithecid from a deposit at Sterkfontein, about a couple of miles from the caves where we are working."[1]

Le Gros Clark (1947a,b) accepted that three genera existed within the Australopithecinae; *Australopithecus* (Dart), *Plesianthropus* (Broom) and *Paranthropus* (Broom). After examining the original material in South Africa, Le Gros Clark stated: "In its[2] anatomical details, however, the bone shows a resemblance to the femur of *Homo* which is so close as to amount to practical identity" (1947a). He further stated that if the fragment had been found in different circumstances it would have been referred to *Homo sapiens* (1947b). In his description and assessment of this specimen Le Gros Clark agreed completely with Broom and Schepers. In a fuller discussion of the anterior extension of the intercondyloid fossa, Le Gros Clark suggested that the notch in its anterior portion was related to pressure from the anterior cruciate ligament in full extension. This would indicate, according to Le Gros Clark, habitual

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1. Again, no specimen number was attached to this specimen. This may be the "Bolt's Farm" femur which has since disappeared from view.

2. This specimen was unnumbered in Le Gros Clark's paper but was TM 1513.

full extension of the knee. He further pointed out that the lateral condyle was larger than the medial, similar to the condition seen in man but opposite to that found in the Anthropoids. It thus seemed likely to him that weight was transmitted as in man, largely through the lateral condyle.

Additionally, Le Gros Clark provided a measure of the degree of shaft obliquity; he suggested that this angle, between the central axis of the femur and the vertical axis, may be of considerable value in discriminating between Anthropoids and man. Le Gros Clark measured tha angle of shaft obliquity by plotting the estimated centre of the shaft taken to the highest point on the intercondyloid notch; he thus estimated the angle of obliquity to be "at least 7 degrees". This is a unique and geometrically unsound way of measuring shaft obliquity. The highest point on the distal articular surface is related to a number of locomotor features but bears no relationship to the geometric centre of the shaft; thus an axis through this point may deviate from the plane of the vertical axis (vide Lovejoy and Heiple, 1970).

Broom and Robinson reported the discovery of a second distal femoral fragment found on June 2, 1948 in the Sterkfontein deposits (Broom and Robinson, 1949). This

specimen, approximately 3" of a lower right femur was found "quite isolated" in the deposits with no other bone nearby; it was said to be nearly perfect except for some breakage on the back of the condyles. The specimen (quite certainly STS 34) "closely resembles the lower femur fragments (sic) found in 1937 and described in 1946". Both Sterkfontein distal fragments differ from man "in the less development of the articular surface on the outer side of the patellar groove". Moreover, in *Plesianthropus* when the condyles rest on a flat surface "The outer part of the anterior surface (of the superior articular surface) is a little lower than the inner" (ibid.); according to Broom and Robinson, this is the reverse of the condition in modern man. They confirmed Le Gros Clark's estimate of the obliquity of the shaft.

Kern and Straus (1949) published a paper suggesting that the distal femoral fragment discussed by Broom and Schepers (1946) and by Le Gros Clark (1947) (unnumbered by them but probably TM 1513) demonstrated a number of "cercopithecid" characters. They arrived at their conclusions without having even seen a cast of the specimen in question, and took their data from Le Gros Clark's paper (1947a). Kern and Straus accepted the conclusions of Broom, Schepers and Le Gros Clark that the fragment resembles the femur of man and differs from that of the anthropoids, "But it remains to be

proven that the characters that it displays are peculiarly and exclusively hominid, and that such characters are necessarily indicative of ability to assume and maintain an erect, bipedal posture" (Kern and Straus, 1949). They further stated that the "*Plesianthropus* fragment is remarkably similar to the femora of the Old World Monkeys" (ibid.).

Their argument rests on five features of the lower shaft of the single specimen: 1) robustness of the femoral shaft; 2) high degree of obliquity of the femoral shaft; 3) the anterolateral surface of the patellar fossa higher than the anteromedial surface; 4) pronounced anterior extension of the intercondyloid notch and 5) the lateral condyle larger than the medial.

It can be seen from their own data, and confirmed in the figures of other workers, that in all but feature No. 2 there are similarities in the lower femoral shafts of some of the Cercopithecoidea, *Plesianthropus* and modern man. It might be suggested, contrary to their conclusions, that the resemblance reflects more the morphology of the generalized primate femur than any close phylogenetic relationship.

The major fallacy of their argument, however, is not the several demonstrable similarities between the

cercopithecid and hominid femora but the ways in which the femora of the two groups differ. For example, in quadrupedal monkeys the extensors show more development than in the hominids since they provide the main locomotor thrust. The development of vastus lateralis, in particular, imprints itself on the anterior and lateral surfaces of the proximal shaft in a way not seen in the hominids. On the posterior surface of the distal shaft of the monkeys the flexors of the knee also show more development than in the hominids; the impressions of gastrocnemius and occasionally plantaris are the best examples of this.

In 1950, Broom, Robinson and Schepers gave a very preliminary description of a further proximal fragment from Sterkfontein. This specimen, 215 mm. long, and representing approximately the "upper 2/3" of a femur[1]. It was said to be "rather badly crushed" (Broom, Robinson and Schepers, 1950). The greater trochanter is lost "but it must have differed in shape from that of the Bushmen, further the trochanteric fossa is not nearly so deep as in man, nor is there a well developed trochanteric crest" (ibid.). The lesser trochanter is "situated somewhat less on the inner side of the femur than in man" so that the femur must have been orientated somewhat differently than in modern man. They estimated the total length to have been 310 mm. and suggested

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1. This specimen apparently is STS 14 (Oakley, et al, 1967).

that this was not too different from the femoral length of living "smaller races of man".

By 1950 the literature contained an abundance of classifications of the South African hominids. Broom (1950) using dental criteria, suggested that three sub-families were represented in the material: the Australopithecinae including the taxa *Australopithecus africanus* (from Taung) and *Plesianthropus transvaalensis* (from Sterkfontein); the Paranthropinae including *Paranthropus robustus* (from Swartkrans) and *Paranthropus crassidens* (from Kromdraai); and the Archanthropinae, with a single taxon *Australopithecus prometheus* from Makapan. He seems not to have noted the inconsistency of including the same genus in two different sub-families.

Washburn and Patterson (1951) suggested that only two genera should be included within the Hominidae: *Homo* and *Australopithecus*. Under this proposal, all the South African material would be included within the single genus *Australopithecus*.

Robinson (1954) rejected this proposal and suggested that the taxon *Australopithecus africanus* should include two subspecies - *africanus* and *transvaalensis* - thus lumping the material from Sterkfontein and Taung together. A second taxon, *Paranthropus robustus*,

should also include two subspecies, *robustus* and *crassidens*, this time lumping the material from Kromdraai and Swartkrans. A third taxon, *Paranthropus palaeojavanicus*, was proposed to include the fossil material from Sangiran.

Bone' (1955) reported the discovery of a hominid femoral head at Makapansgat; it had been found in November, 1949, by A.R. Hughes. Bone' concluded that the fragment seemed "plus forte" to be attributed to *Plesianthropus*; he provided no measurements or pictures with the report. It has since been suggested that this fragment is not hominid (A. Walker, pers. comm.).

It is difficult to agree with Napier (1964) that "The total behavioural pattern provides the basis for taxonomic evaluation". While it is useful to point out that behaviour, as well as morphology and morphologic complexes, should be considered in the formulation of taxonomic categories, the assessment of behaviour in fossil populations is less than entirely objective. Moreover, there is an increasing amount of field data which suggests that social and even locomotor behaviour in some primates is sometimes influenced by the environment (see Jay, 1968 for references). Such data can be interpreted to mean that while the limits of

behavioural responses are genetically determined the manifested behaviour is, to some degree, extrinsically effected. Surely, then,the taxonomic classification of fossil populations must rest with evidence of more intrinsic and less flexible characters than behaviour. In his study of the pelvic and femoral morphology of the early Pleistocene hominids, Napier included three proximal femoral fragments: casts of SK 82 and SK 97[1] and pictures of a single specimen from Sterkfontein (unnumbered, but undoubtedly STS 14). Napier suggested that there are "marked differences in pelvic and femoral morphology between the gracile type and the robust type (which) strongly suggest that evolutionary improvement of walking in the latter is considerably less complete than in the former" (ibid.). A similar conclusion has been reached by Robinson (1967). To support this conclusion Napier pointed out several differences between the two groups. First, the femoral heads of the Swartkrans specimens are said to be small: "The transverse diameter of the head lies well outside that of Bushmen". In contrast, in "the gracile type, as far as can be made out from a published drawing (in Broom, et al, 1950) the head is comparable in size to that of a Bushmen". Yet the head of the Sterkfontein specimen is entirely absent and has been reconstructed

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1. Napier numbered the second specimen "SK 83". SK 83 is a "severely damaged cranium and palate with 6 teeth" (Oakley, et al, 1967). The correct number is SK 97. These specimens appear not to have been formally described and Napier (1964) is the primary reference.

in plaster (see Plate II; also M.H. Day, Pers. Comm.). Napier did not give any actual measurements of the head diameters of the South African specimens, or for his Bushmen comparative group but such data is listed in Table XII. From this data it can be seen that SK 97 is within the Bushmen range and SK 82 lies just outside that range.

A further difference between the Swartkrans and Sterkfontein specimens was said to be that the femoral neck was "relatively much longer than in any human or anthropoid femur studied; in the gracile type, the neck length appears to be comparable to that of a Bushmen". (ibid.). The neck length of the Sterkfontein specimen cannot be ascertained, however, since its proximal termination point is not preserved.

Napier noted several more features on the Swartkrans specimens the condition of which could not be ascertained from the pictures of the Sterkfontein specimen: the small size and lack of flare on the greater trochanter, the absence of a femoral tubercle and an ilio-femoral line. The lesser trochanter was apparently directed backward in both specimens but the trochanteric fossa, deep in SK 82 and 97 is shallow in Sts 14. Thus, the only feature which is demonstrably and observably different between the Swartkrans and Sterkfontein specimens

is the depth of the trochanteric fossa and this single feature hardly seems important enough to validify his conclusions, in view of the poor preservation of the Sterkfontein specimen.

In summary then, it is not denied that these South African femora differ, and differ perhaps significantly, from the femora of *Homo sapiens*. What is denied is that there is demonstrable evidence for suggesting that the Swartkrans specimens differ from the Sterkfontein specimen. On the basis of the evidence Dr. Napier had before him, and even on the evidence available today, there seems to be no clear reasons for separating these specimens on locomotor criteria. This same conclusion has been reached by Zihlman (1971).

In 1967 Le Gros Clark reiterated his earlier statements with regard to the bipedal capabilities of the South African early Pleistocene hominids, as evidenced from the distal femoral fragments. Because of the discovery of a tibia and fibula from Bed I at Olduvai Gorge, he was, however, able to discuss the morphology of the knee joint in slightly more detail than was possible in earlier papers. Drawing on Davis' (1964) assessment of the Olduvai material, Le Gros Clark concurred that the knee joint may have been less evolved in these early forms than it is in modern man. He does

not, however, say how the suggested differences in soleus and popliteus muscles, pointed out by Davis, or the prolongation of the intercondyloid notch may have affected the gait.

Le Gros Clark remained unconvinced of the hominid affinities of SK 82 and SK 97; he stated they were "only doubtfully referrable to *Australopithecus*." (ibid.).

Lovejoy and Heiple (1970) attempted to reconstruct graphically a femur of *A. africanus* using a combination of femoral casts of the Sterkfontein and Swartkrans[1] material. Distal femora used were said to be STS 34[2] and TM 1513. Paradoxically, then, the reconstructed femur of *"A. africanus"* consists, in equal parts, of *A. africanus* (or *Plesianthropus transvaalensis*) and *Australopithecus (Paranthropus) robustus*.

In measuring shaft obliquity they pointed out, as was suggested previously, that by taking the central axis of the shaft through the high point of the intercondyloid notch Le Gros Clark had caused the axial plane to deviate, thus under-estimating the angle of obliquity.

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1. Lovejoy and Heiple, like Napier, erred in referring to SK 83 instead of SK 97.

2. Lovejoy and Heiple stated that Le Gros Clark had used STS 34 in his estimate of the angle of obliquity. Le Gros Clark never numbered the specimen he used and could not have used STS 34 for two reasons: 1) STS 34 was not found until 1948 and therefore could not have been discussed in 1947 and 2) Le Gros Clark clearly stated that he worked with a left femur (1947a); STS 34 is a right femur.

They suggested that the proper procedure would be to continue the axis in the mid-shaft plane to the bicondylar plane, thus more accurately representing this axis. This method has been suggested by others (Pearson and Bell, 1919; Walmsley, 1933). Lovejoy and Heiple estimated the angle of obliquity in the reconstructed femur at 14 to 15 degrees. Using a similar method, Walker has recently obtained a similar value for a reconstructed *Australopithecus* femur (pers. comm.). Using the angle, Lovejoy and Heiple geometrically estimated the total femoral length of 276 mm. for *A. africanus*; this is considerably less than the 310 mm. suggested by Broom, et al (1950). They concluded that their estimate of femoral length is consistent with a body size of 42-43 " and body weight of 40 - 50 pounds. They do not divulge the objective methodology on which these estimates were based.

Lovejoy and Heiple (1972) discussed the several anatomical features of the proximal australopithecine femur which have been said, by various workers, to be distinctive of that group. Admittedly, without having seen the original material and ignoring the crushed condition of STS 14, they stated that the lightly marked intertrochanteric line, the position of the lesser trochanter and the size of the greater trochanter could all be duplicated in their Amerindian

sample. They did not state if all these features could be found together among their comparative group.

III.1.i: COMPARATIVE MATERIALS: The Primary comparative sample was composed of 100 Romano-British femora. This series, from the Ancaster collection in the British Museum (Natural History) was selected only from boxes containing reportedly associated remains of a single skeleton. Only relatively complete, adult femora without obvious pathology were chosen for this study; a further criterion for selection was the inclusion with the remains of at least one-half of the os innominatum. Sexual assessment was made on features of the pelvis as outlined by Hanna and Washburn (1953) and Phenice (1969).

A further sample of 8 Bushmen femora, also from the British Museum (Natural History) was used. Because these are from incomplete skeletons no assessment of sex was made for this series. These bones are also adult and without obvious pathology.

A sample of living Pongids have also been included for comparative purposes. This material was obtained from the British Museum (Natural History) and the Department of Anatomy, St. Thomas's Hospital Medical School. This group, which is adult but unsexed is somprised of *Gorilla gorilla, Pongo pygmaeus, and Pan paniscus.*

III.1.ii: FOSSIL MATERIALS:

Trinil, Femur I: a complete left femur, 455 mm. long, showing very minimal post mortem damage. A small hole in the popliteal surface was caused during excavation.

a 2 cm. long piece was lost from the fossa intercondyloidea and a small fragment was lost from the anterior portion of the medial condyle (Dubois, 1926a). Several possible impressions of "crocodile teeth" are seen on the bone (ibid.). A large osteophytic exostosis extends medially from a point below the lesser trochanter to approximately mid-shaft.

Trinil, Femur II: a right femur which preserves the core of the head and the bases of both trochanters. Cancellous bone is exposed in the core of the head and on the neck. The "lower end is broken off to higher than 4 cm. above the condyles on the backside and the length of the bone in the complete state was at least 4 cm. more than that of Femur I" (Dubois, 1932). The length of the fragment is approximately 400 mm. Its' total length has been suggested to have been 500 mm. (Weidenreich, 1941) or 460 mm. (Day, 1971).

Trinil, Femur III: a left diaphysis, extending from about the level of the lesser trochanter to a position about 2 cm. above the condyles; the total length of the fragment is 320.5 mm. The complete bone may have been about 1.5 cm. longer than Femur I (Dubois, 1932). The total length therefore may have been about 456.5 mm.

Trinil, Femur IV: a right diaphysis broken anteriorly

below the lesser trochanter and posteriorly "more than 2.5 cm. above the patellar surface" (ibid.). The fragment measures 315 mm. and Dubois suggested its full length to have been approximately equal to that of Femur I (ibid.).

Trinil, Femur V : a right diaphysis, 205 mm. long. It is preserved from just proximal to mid-shaft to some distance above the condyles. This may belong to the same individual as Femur III (Dubois, 1934).

The original Javan material was examined in London and at the Rijksmuseum voor Palaeontologie, Leiden, Holland, through the courtesy of Dr. Brongersma, the Director and Dr. D.A. Hooijer.

The problems of dating the Javan specimens has been discussed in Section II.3.ii. Day and Molleson (in press) have concluded that their provenance within the Trinil deposits is supported in general terms but that no irrefutable evidence of their chronometric position is available.

Peking, Femur I : a left proximal diaphysis, 199 mm. long; the total reconstructed length may have been approximately 400 mm. long and it may have been male (Weidenreich, 1941). The specimen was identified in

1938 in a box of antlers which it somewhat resembled since the head and greater trochanter are missing; it may have been excavated as early as 1929 from Locus C[1]. Although Weidenreich did not give the level of Locus C, other material allocated to this site is said to be from the upper levels of Layer 8 (Black, et al, 1933).

Peking, Femur IV : a right femur, preserving almost the entire diaphysis; both trochanters and the head are missing but much of the inferior border of the neck remains. A portion of the suprapatellar fossa is preserved at the distal end; the entire fragment measures approximately 312 mm. and the total reconstructed length has been given as 400 mm. (Weidenreich, 1938); 407 mm. (Weidenreich, 1941; Day, 1971) and 402.5 mm. (Weidenreich, 1941, p. 16). It was first attributed to a female (Weidenreich, 1938) but later referred to as "male" (Weidenreich, 1941). In the earlier publication Weidenreich termed this specimen 'Femur M" as it was derived from Locus M. level 26.

The relevant literature suggests that all of the Peking fossil hominids are broadly contemporaneous and there seems, at the present time, little reason to doubt this supposition. Their attribution to the Middle Pleistocene also seems reasonable on faunal and palynological grounds but it is not possible to make a more finite definition

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1. Locus designations were assigned to fossil material with reference to the order found; they do not relate to the stratigraphic sequence.

of their temporal position within the epoch on the basis of cumently available information.

The only material included in this study which was not studied from original specimens were the seven fragmentary femora from Locality I, Chou-kou-tien; two of these femora are complete enough for inclusion here. The hominids from the Lower Cave at that site are almost universally attributed to a Middle Pleistocene population of *Homo erectus*; the original specimens were presumably lost during hostilities in the 1940's. However, through the kindness of the American Museum of Natural History, Miss Theya Molleson of the British Museum (Natural History) was allowed to bring a complete set of casts, perhaps the only such set in existence, of the Locality I post cranial remains to London. It was from this set of casts and Weidenreich's 1941 monograph that this material was studied. It seems unlikely that any Western scholar still living had an opportunity to examine the remains before their loss and no other paper recording examination of the original post cranial material exists.

Study of the Locality I material posed several important problems- the most obvious of these relates to the impossibility of studying the original material. It would seem preferable, in this case, to use measurements made on the original material even though those measurements,

having been made by a different worker, might incorporate variations due to equipment, individual idiosyncracy and technique. Theoretically preferable, perhaps, but practically impossible in the case of Weidenreich's work. As with his conclusions, discussed in Section II.3.i., Weidenreich's osteometric data also shows internal inconsistency and contradiction. Reference to Table I will show that Weidenreich provided different data sets for the same area of the same bone, in fact, the two data sets did not correspond in a single instance. It was therefore not possible to trust his data and the measurements made for the present study were taken from casts. Moreover, the radiographs are not "X 1" as Weidenreich stated. Plate XX in the 1941 monograph is X 0.93 and Plate XXI is X 0.91 according to measurements on the casts. These corrective factors have been calculated for all measurements obtained from those plates.

Since Weidenreich published radiographs taken only in the anteroposterior position the anterior and posterior cortical thicknesses at the sub-trochanteric and mid-shaft levels could not be derived from his plates. An attempt was therefore made to obtain these diameters from the casts. The anterior and posterior cortical diameters at mid-shaft for Femur I were obtained directly from the cast which is broken at approximately mid-shaft. The sub-trochanteric diameters of Fhmora I and IV and the mid-shaft diameters of Femur IV were not directly obtainable

TABLE I

PEKING

	Measurements from Originals[1]		Measurements from Originals[2]		Measurements from X-Rays[3]		Measurements from Casts[4]	
	Trans.	AP	Trans.	AP	Trans.	AP	Trans	AP
Femur I								
sub-trochanteric	34.3 mm	23.2 mm	29.9 mm	26.7 mm	31.3 mm		33.0 mm	23.4 mm
mid-shaft	29.7	27.1			30.2		30.3	26.5
canal diameter at mid-shaft	9.7	9.9			9.0			
Femur IV								
sub-trochanteric	34.3	22.7			30.3		33.1	23.1
mid-shaft	29.3	25.0	27.8	23.1	26.4		28.8	25.8
canal diameter at mid-shaft	11.1	9.3			8.8			
Femur V								
canal diameter at mid-shaft	8.7	7.5						
mid-shaft	29.5	23.7	27.8	23.6				
Femur VI								
canal diameter at mid-shaft	10.4	9.8						
mid-shaft	29.2	26.1	28.4	25.5				

1. Weidenreich, 1941, page 15
2. Weidenreich, 1941, page 31
3. Weidenreich, 1941, Plates XX and XXI
4. Present study.

from casts of those specimens and the casts of the remaining five femora were therefore examined in the hope of obtaining parameters which could reasonably be translated into the metrical description of Femora I and IV. Table I records the results of these examinations; Femur V has been used as a model for the anterior and posterior cortical diameters at mid-shaft for Femur IV, Femur VI has been used for the anterior cortical diameter at the sub-trochanteric level for both Femora I and IV and Femur VII has been used for the posterior cortical diameter at the same level for both specimens. All of these individuals, according to Weidenreich, were adult males.

OH 20 : a fragment of a left femur consisting of the proximal shaft, parts of both trochanters and most of the neck. It was recovered from the HWK site, Olduvai Gorge in 1959. It was not recovered *in situ* and is possibly from lower Bed II although it may have been derived from upper Bed I (Day, 1969a).

OH 28 : a partial left femur and associated os coxa, found in Bed IV, Olduvai Gorge, in 1970. Almost the entire diaphysis is preserved; the head and greater trochanter are missing but a small part of the inferior border of the neck and part of the lesser trochanter are preserved. The distal end is broken above the popliteal surface (Day, 1971a). The total length of the fragment is 290 mm.

and its reconstructed length may have been 456 mm. (ibid.). The sex of the individual is uncertain since certain contradictory features are present in the associated os coxa. The date of the specimen is approximately .5 m.y. (ibid.).

KNM-ER 736: a left diaphysis preserved from the base of the greater trochanter; the specimen is 288 mm. long. A very small portion of the inferior border of the neck is preserved as it the base of the lesser trochanter. The cortical thicknesses and the disposition of the cancellous tissue suggest that the bone is preserved distally to just above the condyles. It was recovered from "Horizon H" beneath the upper tuff and within the upper unit (Koobi Fora III) at Koobi Fora (Leakey, 1972).

An age of 1.5 to 1.9 m.y. for the Koobi Fora Upper Member has recently been suggested by Maglio (1972). This date is based on trends in molar evolution in *Mesochoerus limnetes and Elephas recki* found in the Rudolf deposits as plotted against values for the same species in the radiometrically dated Shungura formation in the Lower Omo Valley. The data for the two specific lineages agree closely but it must be pointed out that the usefulness of Maglio's correlations rests not only on the validity of the Shungura dates but with the palaeontologist's ability to distinguish ontogenetic and

geographic variability within these populations from intraspecific, secular trends. The dates, however, are reasonable in view of the potassium/argon date of 2.61 ± .26 m.y. for the KBS tuff near the base of the Middle Unit at Koobi Fora (Vondra, et al, 1971; Fitch and Miller, 1970).

KNM-ER 737: a left diaphysis, 369 mm. long, preserving most of the anterior and inferior surface of the neck but without the head and trochanters. The specimen is preserved distally to below the division of the linea aspera into the supracondylar lines; the popliteal surface is markedly convex. It was recovered from the same horizon as KNM-ER 736 (Leakey, 1971).

KNM-ER 738: a left femoral fragment consisting of a well preserved head, neck and proximal shaft. There are two fragments, now joined: the upper fragment, 122 mm. long contains the head, neck and proximal shaft; the distal fragment, 106 mm. long, consists of only the medial aspect of the shaft. The specimen was recovered from Horizon I at Koobi Fora (Leakey, 1971, 1972b). This horizon overlies the unconformity within the upper unit and is beneath Horizon H.

KNM-ER 803: a left diaphyseal fragment, 229 mm. long.

It is preserved proximally to near the top of the gluteal tuberosity and distally to the approximate level of the division of the linea aspera into the medial and lateral supracondylar lines. The specimen consists of two fragments closely joined just distal to the mid-shaft point. There is some loss of cortical tissue through erosion especially on the mediodistal aspect of the shaft. This femur was found associated with two teeth, a fragmented tibia and fibula and a number of foot bones; these specimens were recovered from Horizon D, below the middle tuff at Ileret (Leakey, 1972a). Maglio (1972) has suggested an age range of 1.0 to 1.6 m.y. for the Ileret Member on the basis of faunal evidence.

KNM-ER 815 : a proximal left femoral fragment recovered below the lower tuff at Ileret. The specimen, 107 mm. long is comprised only of the neck and the most proximal portion of the shaft (Leakey, 1972a).

KNM-ER 993 : a right femur, containing most of the diaphysis and distal articular surface. It is sub-adult since the distal epiphysis is not entirely fused. The specimen consists of two fragments in good apposition; the proximal fragment, 141.5 mm. long is continuous from just below the lesser trochanter- the distal fragment, 153 mm. long, joins with the upper fragment below mid-shaft. There is some superficial erosion on the shaft and the medial and

lateral condyles both show some loss of cancellous tissue especially on the inferior articular surface. The specimen was recovered from Horizon A, beneath the upper tuff at Ileret; the age of this tuff has been suggested to be "greater than 1 m.y." on the basis of faunal evidence (Leakey, 1971a) and Maglio (1972) has suggested a range of 1.0 to 1.6 m.y. for this series.

KNM-ER 999 : a virtually complete left femur; it has been reconstructed from a number of well joined fragments. The fragment containing the medial condyle does not join with the distal shaft; however a slight crista indicating the upward extension of the lateral ligament is present on the lateral aspect of the distal shaft and the missing bone is therefore minimal. The total oblique length is estimated to have been 485 mm. The centre portion of the head is present but the margins are absent; the posterior portion of the medial condyle is present but part of the anterior portion is absent and the cortex is abraded on the medial surface. The lateral condyle is not present. The fragments were recovered from near the top of the Ileret sequence. The specimen is unreported.

All of the East African specimens have been examined in Nairobi at the Kenya National Museum through the courtesy of Mr. R.E.F. Leakey, Museum Director.

Omo : a distal right femoral fragment, 71.6 mm. long. It was recovered in 1967 from the KHS site, Member I in the Kibish deposits in the Omo River Valley, Ethiopia (Day, 1969b). It was apparently associated with the very fragmented skeleton of Omo I; this condylar fragment comprises the distal portion of a femur reconstructed from those remains. The date of Member I is uncertain but Butzer, et al (1967), Howell (1968) and Richard Leakey (pers. comm.) agree that it predates the Upper Pleistocene.

Rhodesian, BM(NH) E689 : a left femur, well preserved, in two major fragments. The proximal fragment contains the head and proximal shaft; the total oblique length of this fragment is 190 mm. The distal specimen consists of two fragments, well joined. Both condyles are present although there is some superficial erosion. The total length of this fragment is 180 mm. (Pycraft, 1928).

Rhodesian, BM(NH) E 690: a left diaphysis without proximal or distal articular surfaces; it is comprised of two segments, well-joined. The total length of the specimen is 295 mm; the outer layers of cortical bone show considerable erosion. (ibid.).

These specimens have an estimated age of c. 40,000 years (Oakley and Campbell, 1967).

TM 1513: a distal left femoral fragment, 73 mm. long, recovered at Sterkfontein in 1937 (Broom and Schepers, 1946). There is some erosion on the lateral surface of the condyle but the specimen is otherwise undamaged.

STS 34: a distal right femoral fragment, 61.8 mm. long, recovered at Sterkfontein in 1948 (Broom and Robinson, 1949). It has not been possible to obtain x-rays of the Sterkfontein distal specimens and they have been studied and measured from casts.

SK 82: a well preserved proximal femoral fragment, 145 mm. long.

SK 97: a well preserved proximal femoral fragment, 131 mm. long.

Both the above specimens from Swartkrans have not yet been fully described and although some aspects of their morphology are discussed by Napier (1964) he made no mention of the conditions of their discovery or their suggested date. X-rays of these specimens have been obtained through the courtesy of Dr. Robert Brain; measurements have been taken on the original specimens, according to my techniques, by Professor Michael Day. All of the South African material must be regarded as undated.

Oberkassel: The Oberkassel male (I) and the female (II) were recovered from Magdalenian burials of Late Wurm date; they were discovered in 1914 and reported in 1919 by Verworn, Bonnet and Steinmann. The left femur associated with the male is complete and there is only slight restoration of both trochanters, the medial condyle and the base of the head. The entire proximal portion above the lesser trochanter has been restored on the right femur associated with the female; both condyles and a portion of the distal shaft have also been restored.

Neandertal: the right and left femora associated with the Neandertal skeleton were discovered in 1856 and first described by Schaffhausen in the following year. Their date is "inferred" early Wurm (Oakley, 1964). Both femora are complete and well preserved except for some exposure of cancellous bone on the head and condyles.

The Neandertal and Oberkassel specimens were examined at the Rheinisches Landesmuseum, Bonn, West Germany. Dr. Irwin Scollar, of that Museum, kindly supplied x-rays taken to my specifications.

Spy: The Spy femora, said to be associated with the Spy II skeleton, an adult male, were recovered in 1886 and reported in the same year by Fraipont and Lohest. The

date is given as Wurm I (Zeuner, 1940); the remains were in association with Mousterian tools.

Spy 8: a right femur, complete except for the proximal portion of the greater trochanter.

Spy 16: a proximal left femur, comprising the head, neck and proximal shaft; the total length of the fragment is 280 mm.

Fond-de-Fôret: (Also referred to as "Bay Bonnet") A left femur discovered in 1895 and first described by Tihon in 1898; it was the subject of a very detailed monograph by Twiesselmann in 1961. The specimen comprises approximately the distal 3/4 of the shaft and condyles; all of the proximal articular areas are missing. It was associated with Mousterian tools and is of inferred Wurm date (Twiesselmann, 1961).

The Spy and Fond-de-Fòret femora were examined at the Institut Royal des Sciences Naturelles de Bélgique, Brussels, through the kindness of Professor Twiesselmann. It has not been possible, however, to obtain x-rays of this material.

III.2: OSTEOMETRIC PROCEDURES: Because of the fragmented condition of most fossil femora certain alterations and additions were made in the usual osteometric techniques. New measurements have been formulated, first, in order to deal with the fragmentary condition of much of the fossil sample and second, in the hope of providing parameters which might reflect more clearly the differences between the groups under study.

III.2.i: EXTERNAL MEASUREMENTS:

Length: Length was taken from the base of the greater trochanter at its most distal point on the lateral surface to the horizontal plane of the distal articular condyles. Both condyles were placed against the fixed upright of a standard osteometric board, of Broca's design, with the posterior aspect of the condyles resting on the board; the distal limit of the greater trochanter was located with a small, non-flexible piece of plexiglass and the measurement was read, in millimeters, on the board.

In fossil specimens where the distal end was incomplete the missing length was estimated from the reconstructed length measurements of other workers and by x-ray examination of the cortical thickness of the preserved distal shaft. Comparison of the preserved cortical dimensions on a fossil specimen with similarily located dimensions on complete control specimens would allow a reasonable

estimate of the missing length to be made. Verification of the validity of such comparisons is of course not possible with the fossil sample.

The standard length measurement, oblique length, can be obtained from this measure of shaft and condylar length by using the quotient .142.* This figure was obtained as follows: thirteen femora from the Middlesex Hospital dissecting room were first measured for the maximum anatomical length (fe l_2) by placing them on a standard osteometric board with both condyles in contact with the moveable upright and the head at the fixed upright. Maximum oblique length was then read. The second step was performed, with the bone still in this position, measuring the distance of the base of the greater trochanter from the uppermost point on the head. The base of the greater trochanter is defined as the most distal point where the roughened surface of the trochanter joins the shaft. The function was constructed from the equation:

$$x = \frac{\text{trochanter-head length}}{\text{fe } l_2}$$

and thus represents a mean proportion of the upper length to the total anatomical length of the bone.

The following parameters were taken with sliding calipers

* Standard length = shaft and condylar length plus .142 of shaft and condylar length.

and recorded in millimeters; readings were take to 0.10 mm.

Sub-Trochanteric (Platymeric) Diameters: The maximum transverse diameter was located in the immediate sub trochanteric region with the calipers; a sagittal diameter was then taken at the same level and at approximate right angles to the transverse diameters. This is the method of Martin (1928) and was selected in preference to the method of Manouvrier (op cit) in order to reflect more accurately the maximum width of the upper shaft. Observation has indicated that the sagittal diameter varies little in the sub-trochanteric level but the width of the upper shaft may vary considerably through a vertical range of 2 to 3 cm. In taking the sagittal diameter the gluteal ridge was avoided.

Mid-Shaft (Pilastric) Diameters: The maximum sagittal diameter, perpendicular to the vertical axis of the specimen was taken where ever it occurred in the mid shaft area. A transverse diameter was then taken at the same level and at approximate right angles to the sagittal diameter.

Lower Mid-Shaft (Sub-Pilastric) Diameters: the vertical position of the measurement is defined at 70% of the length as described previously. The position was defined

on the bone, using a steel centimeter tape, extending from the base of the greater trochanter along the lateral surface of the specimen. A sagittal diameter was taken with calipers and a transverse diameter was then taken at the same level and at approximately right angles to the sagittal diamters.

Lower (Popliteal) Diameters: The vertical position of this measurement is defined as 85% of the length of the bone as described previously. The position was defined on the bone in the same way as described above. A sagittal diameter was taken with sliding calipers and a transverse diameter was then taken at the same level and at approximately right angles to the sagittal diameter. This vertical point will generally fall 3 to 4 cm. above the anterior superior articular border of the external condyle; this is the position at which the popliteal diameters are generally taken (Manouvrier, Hepburn, Pearson and Bell, op cit), however, since the condyles are missing or imperfectly preserved in most fossil specimens the present method was felt to be preferable.

Circumference: The circumference was measured with a steel tape at the level of the mid-shaft (pilastric) diameters.

Minimum Transverse Breadth: This was located by moving the calipers vertically along the medial and lateral

surfaces of the femur until a minimum reading was obtained. Care was taken to ensure that the measurement was taken at right angles to the anteroposterior plane through the linea aspera. The point of minimum breadth was marked on the lateral aspect of the bone; the height of this point above the lower-most extremity of the lateral condyle was then measured with a steel tape.

Bicondylar Breadth: Taken parallel with the infra condylar plane with the bar of the calipers touching the lowest points of both condyles and the arms of the calipers recording the maximum distance between the most lateral aspect of the lateral condyle and the most medial aspect of the medial condyle.

Maximum Length of the External Condyle: The maximum anteroposterior length of the external condyle taken parallel with the infra condylar plane.

Maximum Length of the Internal Condyle: As above.

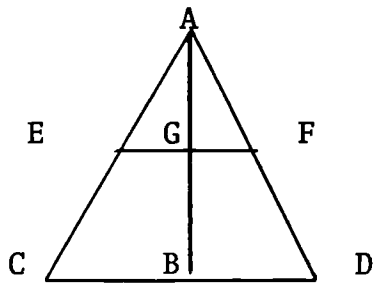
Maximum Breadth of the External Condyle: This records the maximum breadth of the articular surface of the external condyle in the mediolateral orientation and parallel with the infra condylar plane.

Maximum Breadth of the Internal Condyle: As above.

III.2.ii: RADIOGRAPHIC PROCEDURES: Radiographs were made for the purposes of measurement and examination on all femora included in this study. Two views were taken of each bone. An anteroposterior view was taken with the bone resting directly on the film on the posterior surface of the distal condyles and the posterior portion of the greater trochanter. In this position a plane through the linea aspera is at approximately right angles to the film surface and in the absence of the condyles the specimen was oriented with the linea aspera in this position. Incomplete specimens were fixed in position with foam wedges which are not radiopaque. A lateral view was made with the bone resting on its lateral surface and oriented so that a plane anteroposteriorly through the linea aspera would be parallel with the film surface. Incomplete specimens were secured as described above. Strip film, 124 mm. wide, encased in light proof paper and without cassette was used for the comparative sample. A soft cone and a focal distance of 90 cm. were used throughout the study.

In any photographic process where the object is not in direct physical contact with the film, distortion of the object through magnification will occur. This magnification can be minimized either by reducing the object-to-film distance or by increasing the focus-to-film distance. The amount of image magnification

occurring can be estimated with trigonometric methods. Thus:



A = Source

EF= Dimension of Object

CD= Dimension Recorded on Film

Therefore: $\frac{CD}{EF} = \frac{AB}{AG}$

This demonstrates that the ratio of image size to object size is equal to the ratio of focus-to-film distance to focus-to-object distance. From this the amount of magnification can be calculated:

$$\frac{\text{Focus-to-film distance}}{\text{Focus-to-object distance}} = \text{Magnification Factor}$$

(Jaundrell-Thompson and Ashworth, 1970).

In the present study, the focus-to-film distance was a constant 90 cm; if the anterior surface of the mid shaft point is taken as the terminus of the focus-to-object distance then the magnification factor can be calculated. For the largest bones the height of the

anterior surface of the mid-shaft point above the film is approximately 6.5 cm; for smaller and/or incomplete specimens this distance may be as little as 3 cm. When calculated with the formula, the Magnification Factor can be seen to vary between 1.03 and 1.08. It is assumed that the small range of 0.05% in the Magnification Factor will not significantly affect the results.

All radiographs, except those of SK 82 and SK 97, were made expressly for this study and at my instructions. In the case of the South African specimens the radiographic techniques were similar enough and the specimens important enough to warrant their inclusion in this study even though strict control over procedure was not possible. The smaller focus distance of 80 cm. was included in the calculations when the measurements were made on the x-rays. The Peking femora, of course, presented special problems and details of the radiographic study of this material can be found in Section III.1.ii. The technical details of the radiography varied throughout the series due to different degrees of fossilization or demineralization; this data can be found in Table II.

X-rays of the comparative sample were examined and measured on an ordinary Kodak x-ray viewing box. X-rays of the fossil specimens were examined and measured, however, with the aid of a Kodak High Intensity Illuminator.

TABLE II

RADIOGRAPHIC DATA

SPECIMEN	KV	MA	EXPOSURE TIME	CONE DISTANCE	RADIOGRAPHER	OTHER INFORMATION
Ancaster Series	70	6	2 x 60	90 cm.	Kennedy	Agfa Structurix DF, Strip Film, Hard Cone
Bushmen Series	50	5	1 x.02	"	Kennedy	"
Pan	50	6	1 x.02	"	"	"
Pongo	50	6	1 x.02	"	"	"
Gorilla	50	3.2	1 x.02	"	"	"
Oberkassel	70	3	5 x 60	"	Dr. Joachim, Rh. Landesmus. Bonn, We. Germ.	
Neandertal	70	3	5 x 60	"	"	
OH 28	65	6		"	Dr. A. Walker	
KNM ER 737	65	6		"	"	
KNM ER 736	62	5		"	"	2 mm. Aluminium Screens
KNM ER 803	70 65	7.5(AP) 6.0(ML)		"	"	
KNM ER 993	70 62	9 (AP) 5 (ML)		" "	" "	

TABLE II

(continued)

SPECIMEN	KV	MA	EXPOSURE TIME	CONE DISTANCE	RADIOGRAPHER	OTHER INFORMATION
KNM ER 999	70 62	9(AP) 5(ML)		90 cm.	A. Walker	
Rhodesian (BMNH 689)	80	6	6 x 60	"	T. Molleson	Agfa RP Film; .004 mm. Lead Screens
Rhodesian (BMNH 907)	80	6	6 x 60	"	"	"
Rhodesian (BMNH 690)	85	6	10 x 60	"	"	Kodak Blue Brand; .004 Lead Screens
SK 82	80	200		80 cm.		Blue Brand Film; 1 mm. Lead Screens
SK 97	80	200		80 cm.		"

Every care has been taken to insure that the external and internal measurements were made at the same level on the bones. In the Ancaster, Bushmen, Pongids and East African fossil specimens the position at which the external parameters were taken was marked with a radiopaque lead tape manufactured by 3M. Such marking was not possible on the Oberkassel, Neandertal, Trinil and Swartkrans femora. In these cases, note was made of the distance of the external parameters from a landmark which would later be identifiable on the x-rays. Thus, in complete specimens the lower margin of the internal condyle was used; in fragmentary specimens the mediodistal edge or a distinguishing fracture line was used.

The following measurements were made on the radiographs; measurements were taken with calipers to 0.10 mm.

Sub-Trochanteric (Platymeric) Level: On the anteroposterior x-ray view: medial and lateral cortical diameters at the level of the external diameter. On the lateral x-ray view: anterior and posterior cortical diameters at the level of the external diameter.

Mid-Shaft (Pilastric) Level: On the anteroposterior x-ray view: medial and lateral cortical diameters at the level of the external diameter. On the lateral

x-ray view: anterior and posterior cortical diameters at the level of the external diameter.

Lower Mid-Shaft (Sub-Pilastric) Level: On the antero-posterior x-ray view: medial and lateral cortical diameters at the level of the external diameter. On the lateral x-ray view: anterior and posterior cortical diameters at the level of the external diameter.

The following three measurements were made to determine the amount of anteroposterior bowing of the femoral shaft and the point of maximum subtense in relation to femoral length. Using the lateral x-ray view, a chord was inscribed on the film with a scalpel from the level of the anterior sub-trochanteric measurements to the level of the anterior popliteal measurements, which although the latter were not included in the x-ray parameters, had been marked with lead prior to x-raying.

Bowing: This is reflected in the length of the maximum subtense from the chord to the anterior border of the shaft; measured with calipers.

Length of the Chord: The distance from the point of the anterior sub-trochanteric measurements to the point of the anterior popliteal measurements. Taken with a transparent millimeter rule.

Distance of the Foot of the Subtense from the Lower Terminus of the Chord: taken with a transparent millimeter rule.

Vertical Head Diameter: the maximum vertical head diameter taken with a transparent millimeter rule.

Head-Neck Axial Length: the mid-points of the shaft at the levels of the sub-trochanteric and sub-pilastric indicators were marked with a scalpel. The mid- shaft axis was then marked, with a scalpel, and continued upward into the proximal shaft. The mid-points of the head and neck were then marked on the same plate, again with a scalpel. The length of the head-neck axis was then read, with a transparent millimeter rule, from the peripheral margin of the head, through the mid points of the head and neck, to the point of intersection of this axis with the mid-shaft axis.

This measurement was used in preference to simple neck length for two reasons. The length of the head-neck axis represents a functional unit and neck length, by itself, is only a component of that unit. Second, is the difficulty in accurately measuring neck length. In fossil specimens the margins of the head are nearly always

eroded and a precise estimate of neck length at either its junction with the head or the shaft is very imprecise.

Twelve indices have been formed from these parameters. Numbers 1,2,4,5 and 6 represent standard indices included in many other studies on the femur; numbers 3 and 7 through 12, however, are new indices. The analysis of the data has shown those parameters which tend to maximize the differences between the groups included in this study. These indices have therefore been formed from those parameters which show the largest F values and the largest mean group differences.

1. Platymeric Index:

$$\frac{\text{100 x anteroposterior diameter in the sub-trochanteric area}}{\text{transverse diameter in the sub-trochanteric area}}$$

2. Pilastric Index:

$$\frac{\text{100 x anteroposterior diameter in the mid-shaft area}}{\text{transverse diameter in the mid-shaft area}}$$

3. Sub-Pilastric Index:

$$\frac{\text{100 x anteroposterior diameter at 70\% of shaft length}}{\text{transverse diameter at 70\% of shaft length}}$$

4. Popliteal Index:

$$\frac{\text{100 x anteroposterior diameter at 85\% of shaft length}}{\text{transverse diameter at 85\% of shaft length}}$$

5. Head and Neck Index:

$$\frac{\text{100 x vertical diameter of head}}{\text{length of head-neck axis}}$$

6. Neck-Shaft Index:

$$\frac{\text{100 x head-neck axis}}{\text{shaft length}}$$

7. Minimum Breadth Index:

$$\frac{100 \times \text{height of minimum breadth above the condyles}}{\text{shaft length}}$$

The following indices have been formed in part from the internal parameters taken from the x-rays.

8. Transverse Platymeric Cortico-Medullary Index:

$$\frac{100 \times (\text{medial cortical diameter in the sub-trochanteric area} + \text{lateral cortical diameter at the same level})}{\text{total transverse diameter in the sub-trochanteric area}}$$

9. Sagittal Platymeric Cortico-Medullary Index:

$$\frac{100 \times (\text{anterior cortical diameter in the sub-trochanteric area} + \text{posterior cortical diameter at the same level})}{\text{total sagittal diameter in the sub-trochanteric area}}$$

10. Transverse Pilastric Cortico-Medullary Index:

$$\frac{100 \times (\text{medial cortical diameter in the mid-shaft area} + \text{lateral cortical diameter at the same level})}{\text{total transverse diameter in the mid-shaft area}}$$

11. Sagittal Pilastric Index:

$$\frac{100 \times (\text{anterior cortical diameter in the mid-shaft area} + \text{posterior cortical diameter at the same level})}{\text{total sagittal diameter in the mid-shaft area}}$$

12. Cortical Robusticity Index:

$$\frac{100 \times (\text{anterior cortical diameter in the mid-shaft area} + \text{posterior cortical diameter at the same level})}{\text{shaft length}}$$

III.2.iii: NON-METRIC VARIABLES: Each of the femora included in this study has been graded for the appearance of non-metric variables. Although epigenetic, discontinuous variables of the skull in *Homo sapiens* have been treated with multivariate statistical methods (Brothwell, 1959; Laughlin, 1963; Berry and Berry, 1967; Berry, 1968; Kellock and Parsons, 1970a,b) such an approach seemed inappropriate in the present study. The primary reason for this is that whereas the above studies on the cranium used a comparatively large number of observations this study considered only five variables. Therefore, the relationships between the variables in this study could easily be demonstrated with more prosaic, univariate displays. Second, the epigenetic features analyzed by Berry and Berry and Kellock and Parsons were placed in present or absent categories. In the present study it was felt that too much information would be lost through such discrete categorization and it was preferable, therefore, to treat the non-metric variables in a gradational manner. Finally, although some workers have suggested that the distance values obtained from non-metric variables are more valid than those obtained from metric variables (see especially Brothwell, 1965) this view has recently been seriously questioned through the results obtained by Rightmire (1972a).

Five features of the femur were included in this analysis; these were selected for inclusion primarily because it had been suggested by earlier workers that the incidence and development of these features may have differed in fossil hominids and modern sapient populations. Weidenreich (1941) for example, suggested that the third trochanter and fossa and crista hypotrochanterica were more developed in the Peking fossil hominids than in his modern comparative sample; he did not, however, provide figures to support his conclusions. He similarily suggested that the upward extension of the linea aspera into the base of the greater trochanter was a unique feature of the Peking specimens. Dubois (1895, 1926a) stated that the curved, convex popliteal surface of '*Pithecanthropus*' *I* was a "feature not found in modern man". Although numerous workers have disagreed, the feature has been the subject of wide enough discussion to warrant its inclusion here.

In establishing the grades of development of the third trochanter and fossa and crista hypotrochanterica the entire Ancaster series was laid out for examination. Prototypes for the grades "slight", "moderate" and "marked" were selected from the entire series and were used as referant models throughout the study. As in any system which attempts to arbitrarily divide continuously variable features, specimens showing

intermediacy in development posed difficult problems. However, by constant reference to the type series it is felt that most bones have been allocated to the category they most closely resemble and a high degree of internal consistency has been maintained.

Assessment of the curvature of the popliteal surface was not arbitrary, however, and the three categories "convex", "plane" and "concave" were clearly determinable on most specimens with the aid of a flat-edged piece of plexiglass. In specimens where the shape of this feature was equivocal a small level was placed on the popliteal surface and this indicated, without question, the presence or absence of curvature. The assessment of popliteal curvature was made, in all cases, at the level of the popliteal measurements; i.e. at 85% of the length of the femur.

The assessment of the upward extent of the linea aspera was similarily entirely objective. The feature was graded as "continuous" if a ridge or crista was visually or tactilly detectible in the area immediately below the greater trochanter. If the bone was smooth in this area and a clear gap existed between the top of the linea aspera and the base of the greater trochanter the feature was graded as "discontinuous".

The distribution of the non-metric characters has been

statistically evaluated to assess the significance of the group figures. In performing goodness of fit calculations on non-parametric data comprised of more than two classes an important difficulty arises in defining the expected frequencies necessary in x^2 (chi^2) formulae. In many instances, estimated frequencies for biologic variables can be determined through the use of Mendelian ratios and other estimates of expected proportions, extrapolating from the known, or hypothesized genetic etiology of the feature under consideration. Such use of extrinsically estimated frequencies is widely applied in genetic studies. In the present study,however, the etiology, genetic or ontogenetic, is not known and the estimated frequencies had to be determined from intrinsically hypothesized data. For this purpose the Brandt-Snedecor formula for x^2 seemed most appropriate. The formula is:

$$x^2 = \frac{\sum \frac{a^2}{n} - \frac{A^2}{N}}{k\,(1-k)} = \frac{\sum \frac{b^2}{n} - \frac{B^2}{N}}{k\,(1-k)}$$

When:

a,b = data frequencies
A,B = sample totals
k = A/N
1-k = B/N

(Bailey, 1959)

Although Socal and Rohlf (1969) suggest the removal of a total of a-3 degrees of freedom for the use of

intrinsically derived expected frequencies this seemed inappropriate in the present study. After the usual removal from the class total of one degree of freecom for the sum of the frequencies Sokal and Rohlf suggested the removal of two further degrees of freedom: one removal for the estimate of the means and one for the estimate of the standard deviation. However, since the x^2 figures are calculated, in this study, from non-parametric data this step seems unnecessary and the degrees of freedom are based on a-1. All x^2 figures were obtained on a desk calculator programmed for such calculations.

III.3: ANALYTIC METHODS: The data gathered for this study will be analyzed through several analytic methods including multivariate statistics. Although multivariate statistics have been widely criticized, more for their application than their theory, they remain the only method by which the volume of data comprising a study such as this can be examined and evaluated as a whole. No method which relies on selected parameters and samples can be termed truly objective yet through analyses such as these a strong element of objectivity is interjected.

The multivariate methods used in this study are basically the statistics of discrimination and distance; these methods developed out of the realization that the central tendency modes and frequencies of the typologists were no longer appropriate to classificatory schemes bases on the concepts and constructs of population variability. Where univariate analyses were adequate to deal with taxonomic questions of a typologic nature the simultaneous consideration of multiple parameters is necessary for the newer approaches embodied in the synthetic theory of evolution.

An early attempt to discriminate between samples using multiple variables was made by Karl Pearson in 1926; For the remainder of that decade and throughout the

the thirties Pearson, and Morant, continued to develop and apply the Coefficient of Racial Likeness (CRL) to a wide variety of human specimens and populations. The CRL was criticized by Fisher (1936) who noted that this method was not a true estimate of biologic distance but rather represented the degree of probability that the samples were drawn from the same populations. Moreover, Fisher also pointed out, as have many others, that the CRL did not take into account the amount of correlation between the included variables. Thus, in small but significant correlations genetic and functional interrelations may be overlooked and, on the other hand, highly correlated variables may be weighted out of all proportion to their relevance to the particular problem under study. These difficulties were overcome by the analyses based on the discriminant function first proposed by Barnard (1935) and by Fisher, later in the same year.

Discriminant function analysis is a method which defines the probability that a specimen is included in one of two or more pre-determined and pre-defined groups. It is mathematically and theoretically similar to the multiple regression formulae used by Pearson and others for a variety of posterior probability problems. Discriminant function analysis uses (say) t variables for k groups containing n numbers and

from the means and standard deviations computes the average sum of the squared differences for the t variables between the groups. Thus:

$$w = V^{-1}d$$

When: w = vector of weights (or probability)

V = weighted average of the dispersion matrices

d = vector of differences between t pairs of means for the included groups.

(Hope, 1968)

Discriminant function analysis has been used by Bronowski and Long (1952) in order to evaluate the probability that *Australopithecus* belonged to either the Pongidae or the Hominidae. From their study, based on four measurements of the deciduous canine, they concluded that the results "prove conclusively that these teeth do not belong in the ape category". Moreover, "they fall precisely in the human range" (ibid.).

Two criticisms must be made at this point: the first applies to discriminant function analyses in general and the second applies specifically to the study of Bronowski and Long. This method of analysis utilizes

pre-arranged and pre-defined groups and the possibility (or probability) that the specimen in question belongs to other than the *a priori* groups is not considered. Therefore, on the basis of these results, *Australopithecus* had to be assigned to either the Hominidae or the Pongidae and it was not possible to test the hypothesis that the specimens belonged to yet a third group. Fisher, while applying the method to taxonomic problems (1936, 1938) recognized the usefulness of discriminant functions in assigning specimens to all-inclusive groups such as sex, and this is undoubtedly where the greatest validity and usefulness of the method in Anthropology lies. Pons (1955), Thieme (1957), Giles and Elliott (1963) and Giles (1963) have applied discriminant function analyses to problems of the sexual definition of human material. The second criticism of Bronowski and Long's work is that taxonomic allocations, even at the family level, cannot validly be made on the basis of four measurements of a single tooth. Ashton, Healy and Lipton (1957) attempted to deal with this problem by increasing the number of parameters (using 4 to 8) and the number of teeth (using 8 teeth of the permanent dentition). Instead of using Fisherian discriminant functions they based their analysis on the generalized distance statistic (D^2) and on canonical analysis. With

the increased number of parameters and specimens, Ashton, et al, found that they could not conclusively assign the australopithecine material to either the Hominidae or the Pongidae. The fault with this approach lies with the author's neglect of the importance of the total metrical description of the entire dentition, thereby ignoring the most basic advantage of multivariate analyses. It is the total pattern of the system as a whole which is important in taxonomy and not the metric morphology of the component parts.

The generalized Distance Statistic (D^2) was proposed in 1930 by Mahalanobis. Mathematically it is very similar to Pearson's CRL; however, it has the very important advantage of having the ability to decorrelate the variables so that redundant dependent biometric information is not included in the analysis. Thus, for p variates D^2 is defined as:

$$D^2 = \sum_{i=1}^{p} \sum_{j=1}^{p} s^{ij} d_i d_j$$

When: $d_i = \bar{x}_{ia} - \bar{x}_{ib}$ (i.e. mean character i in population a minus mean character i in population b)

$s^{ij} = (s_{ij})^{-1}$ (i.e. the inverse of the common dispersion matrix)

(Mahalanobis, 1936).

Although Mahalanobis's early distance formulae structure

provided methods of decorrelation, Rao (1941, 1948) provided the method now generally in use. This method consists of a series of linear transformation equations which alter the correlated dependent variables into decorrelated, independent variables. This method arbitrarily takes as its first transformed variable (Y_1) and subtracts from a second variable an amount proportional to its correlation with (Y_1); the result is the second transformed variable (Y_2). The process is repeated until (Y_p) is equal to the number of variables included. Thus:

$$Y_1 = m_1$$

$$Y_2 = m_2 - a_{21}Y_1$$

$$Y_p = m_p - a_{pp-1} \ldots - a_{p1} Y_1$$

When: p = number of variables
m = normalized mean deviations for a given group
a = coefficients to decorrelate Y

(Rao, 1948)

A further advantage of D^2, and one of particular importance in dealing with small, fossil samples is that it provides a method whereby the final biased

estimate of population distance can be corrected for small sample size. This alteration is a function of the number of individuals and variables included in each cohesive sample. Thus:

$$p\left(\frac{1}{n_i} + \frac{1}{n_j}\right)$$

is subtracted from the biased D^2 figure for each sample.

Although non-weighted variables are very important in estimates of overall biometric distance the decorrelation procedures may obscure important functional relationships. Here inspection of the correlation matrices is of vital importance in revealing such patterns of relationships.

D^2 is an especially attractive estimate of population distance since studies on living groups have verified, to some extent, its reliability in indicating biometric distance. This efficacy has been demonstrated in a number of studies in which biometric distances based on this function have favorably compared with affinity estimates of earlier workers based on linguistic and cultural evidence. Such confirmatory results have been published by Trevor (1950), Jones and Mulhall (1949), Talbott and Mulhall (1962), Hanna (1962) and

Rightmire (1972b). Additionally, Huizinga (1965), using eight cranial measurements found that D^2 correctly paired 60% of a group of fathers and sons. The Generalized Distance Statistic has also been widely used in less verifiable situations involving fossil hominids. Weiner and Campbell (1964), Day (1967), Day and Wood (1968, 1969), Rightmire (1972a) have all used D^2 in order to relate a fossil specimen to other specimens and populations; Bilsborough (1971) following Van Vark (1970) has used D in preference to the squared function.

There can, however, be no assurance that estimates of biometric relationships and distances within a single anatomical unit, such as that used in this study, relate to affiliations of taxonomic significance. The very fortuituous nature of the survival of palaeontologic material suggests the possibility that the means of the fossil population have not been sampled; rather very random points along the spectrum of what may be very considerable population variability may represent the basic components of the fossil sample. The "mean" therefore determined for the purposes of discrimination may in fact represent a point some distance along the spectrum away from the actual population mean.

The multivariate analysis of the entire sample was performed through a stepwise discriminant analysis, the BMD 07M program. The program includes not only stepwise discrimination, to indicate the variables most contributory to the differences between the groups, but also provided within groups covariance and correlation matrices, D^2 values and plots the first canonical axis against the second. F values and the U statistic are also provided to test the equality of the group means.

IV.1: RESULTS OF THE EXAMINATION OF THE NON-METRIC VARIABLES: These results are presented graphically in Tables III to VII. Table VIII gives the x^2 significance values for this data in the Ancaster population, the only group large enough for significance testing. Table VIII shows that none of the x^2 values for the Ancaster series is significant above the p= .05 level; however, x^2 significance levels for sexual difference in the development of the gluteal fossa and third trochanter show levels just below the p= .05 level (the critical level with three degrees of freedom = 7.815). This suggests the possibility that in a yet larger sample these features might show significant values with regard to sex.

The distribution of the three categories of the shape of the popliteal surface (Table III) suspiciously resemble a nearly perfect Mendelian ratio of 1:2:1 with the "heterozygotes", showing concavity, having 51% of the total distribution. Since this feature seems not to be explainable on the basis of sex or side its genetic etiology might bear further investigation. Table III shows that the convex popliteal surface, while common in the fossil specimens under consideration here, is not a universal feature of the early hominid femur. Furthermore, it might be argued

TABLE III
Shape of Popliteal Surface

	Part Absent	Concave Rt	Concave Lt	Concave M	Concave F	Flat Rt	Flat Lt	Flat M	Flat F	Convex Rt	Convex Lt	Convex M	Convex F	Totals Concave	Totals Flat	Totals Convex
ANCASTER N=100 M=60 F=37																
BUSHMAN N=15																
ANTHROPOIDEA																
Pan N=3														X		
Pongo N=3														X		
Gorilla N=3															X	
FOSSIL HOMINIDAE																
Neandertal																
Rt																X
Lt																X
Oberkassel																
Rt														X		
Lt														X		
Rt														X		
Spy																
8																X
16	—															
Rhodesian														X		
Trinil, Femur I																X
II																X
Peking, Femur IV															X	
OH 28	—															
KNM-ER 736	—															
737																X
738	—															
803	—															
993														X		
999														X		
SK 82	—															
SK97	—															

TABLE IV

DEVELOPMENT OF THIRD TROCHANTER

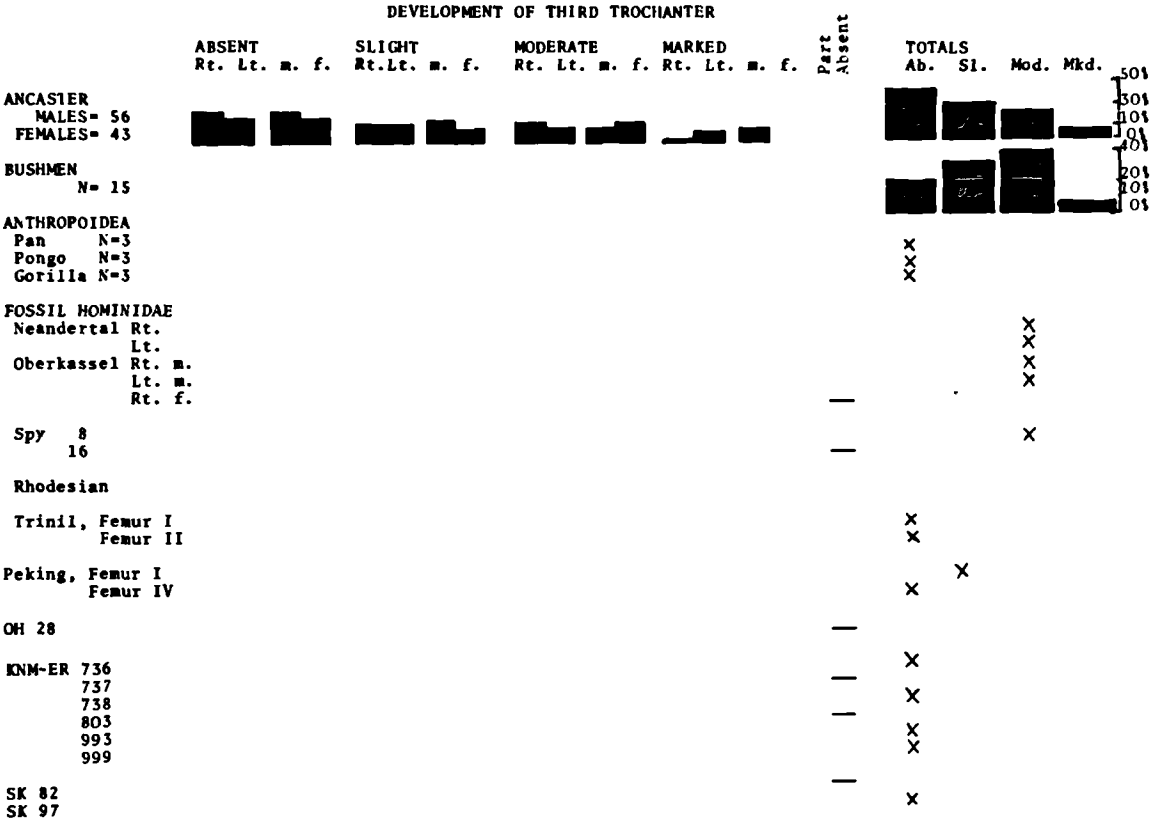


TABLE V
DEVELOPMENT OF HYPOTROCHANTERIC CRISTA

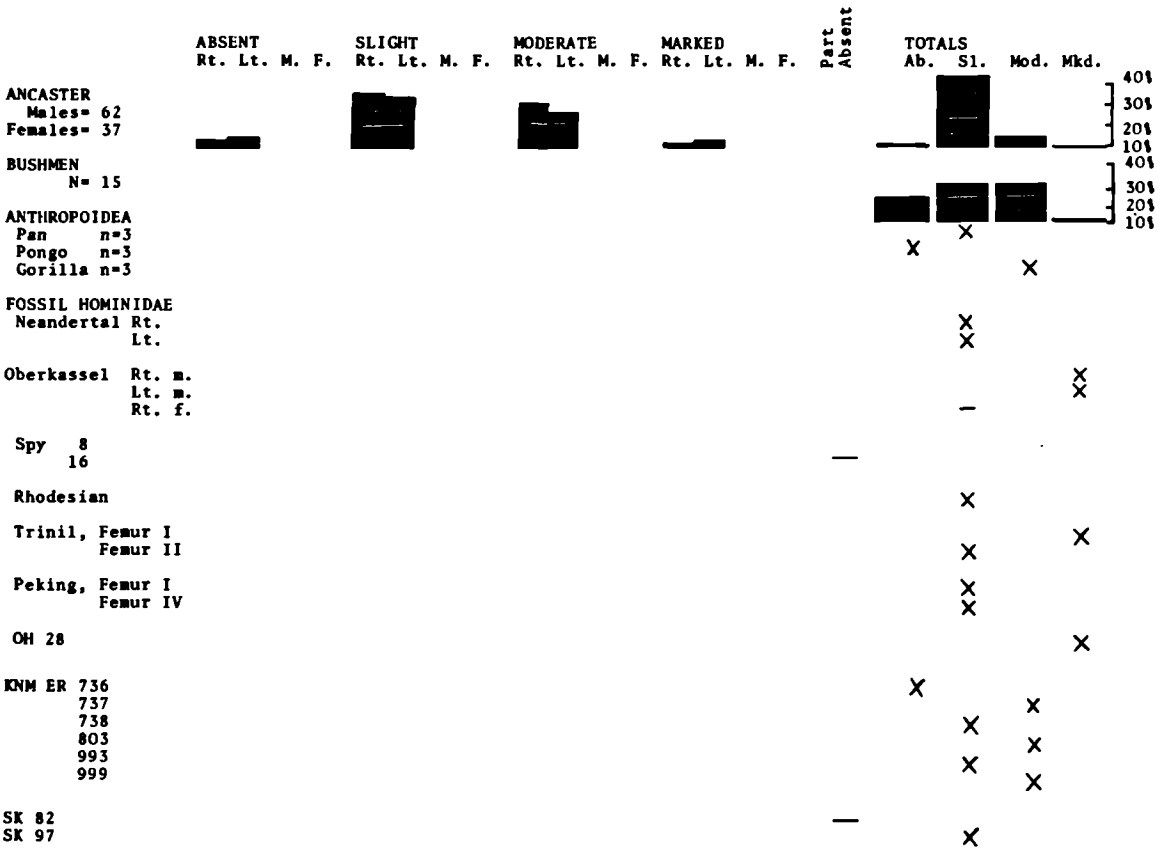


TABLE VI

DEVELOPMENT OF HYPOTROCHANTERIC FOSSA

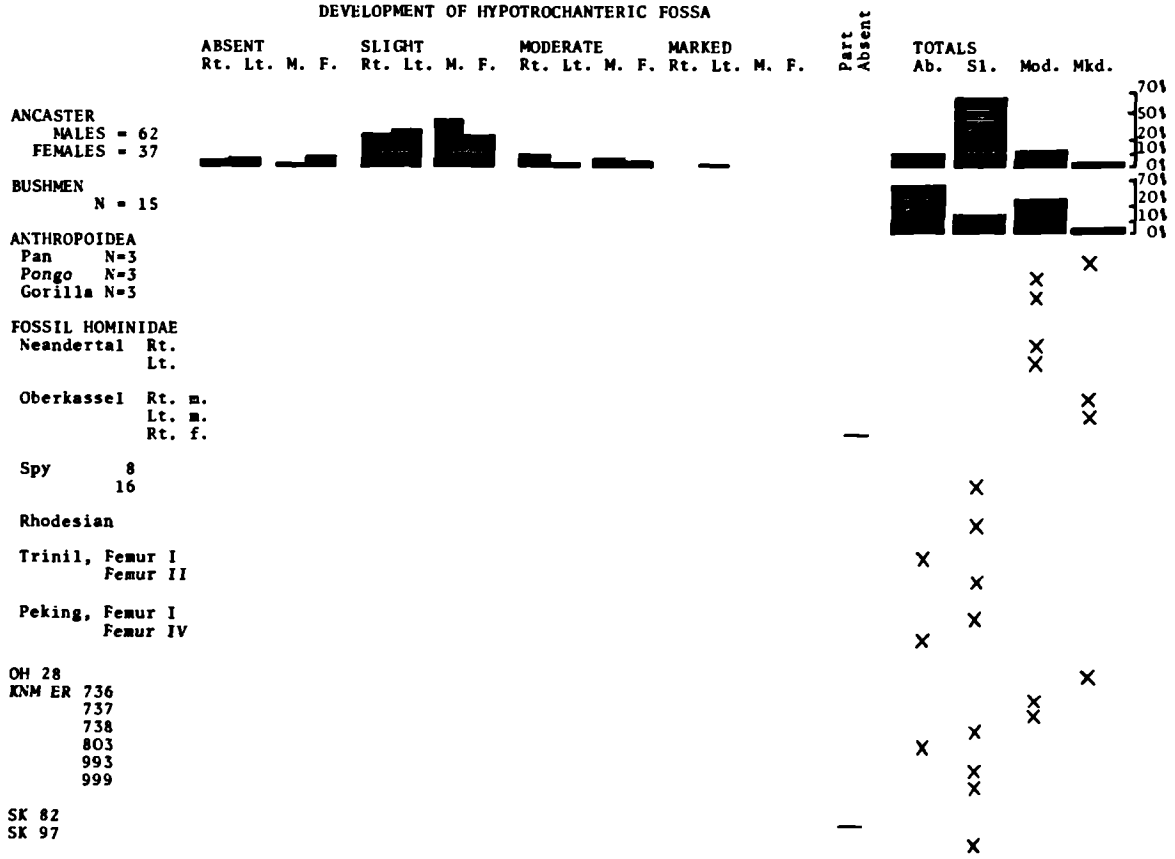


TABLE VII

UPWARD CONTINUATION OF LINEA ASPERA

	Part Absent	CONTINUOUS Rt.	CONTINUOUS Lt.	CONTINUOUS M.	CONTINUOUS F.	DISCONTINUOUS Rt.	DISCONTINUOUS Lt.	DISCONTINUOUS M.	DISCONTINUOUS F.	TOTALS Cont.	TOTALS Disc.
ANCASTER MALES =61 FEMALES =38											
BUSHMEN N=15											
ANTHROPOIDEA											
Pan N=3	—										
Pongo N=3	—										
Gorilla N=3	—										
FOSSIL HOMINIDAE											
Neandertal Rt.										×	
Lt.										×	
Oberkassel Rt. m.										×	
Lt. m.										×	
Rt. f.										×	
Spy 8										×	
16										×	
Rhodesian											×
Trinil, Femur I										×	
Femur II										×	
Peking, Femur I											
Femur IV										×	
OH 28											×
KNM ER 736	—										
737	—										
738											×
803	—										
993	—										
999											×
SK 82											×
SK 97											×

TABLE VIII

CHI^2 VALUES FOR NON-METRIC VARIABLES

ANCASTER SERIES

CHARACTER	DEGREES OF FREEDOM	CHI^2	SIGNIFICANCE
Popliteal Conformation			
Side	v = 2	+0.695	P = < 0.5
Sex		+3.779	P = < 0.1
Continuity of Linea Aspera			
Side	v = 1	+0.163	P = < 0.5
Sex		+1.630	P = > 0.5
Development of Hypotrochanterica Crista			
Side	v = 3	+0.847	P = > 0.9
Sex		+5.123	P = < 0.1
Development of Third Trochanter			
Side	v = 3	+2.571	P = > 0.5
Sex		+7.312	P = < 0.05
Development of Hypotrochanterica Fossa			
Side	v = 3	+4.442	P = < 0.1
Sex		+7.631	P = < 0.05

(Critical values for x^2 from Rohlf and Sokal, 1969)

that the much discussed convexity of the popliteal surface in Femur I, from Trinil is related to the pathology which so markedly affected other areas of the shaft. It is difficult to attribute great locomotor significance to this feature since the Pongid femora, like the majority of the hominid femora, are concave.

The results of observations on the hypotrochanteric fossa are presented in Table IV. The results show that while the "slight" category is most common both in Ancaster and the fossil hominids, the "absent" category is most common in the Bushmen. Table VIII shows that the x^2 level in the Ancaster sample is just below the p= .05 significance level and may, therefore, be related in a general way, to male robusticity. Indeed, the only examples of marked development found in the fossil specimens were in the Oberkassel male, an extremely robust individual, and in OH 28.

The term generally applied to this feature, the gluteal fossa, is incorrect since other muscles besides gluteus maximus are attached here.

The development of the hypotrochanteric crista does not show a mathematical distribution like that of the fossa hypotrochanterica and here the significance

level for sex is much less important. Again the "slight" categories show greater preponderance in both Ancaster and the fossil specimens. The "slight" and "moderate" categories show identical numbers in the Bushmen. In the "marked" category, Oberkassel and OH 28 have been joined by Trinil, Femur I but in the latter case the development of the crista may have been influenced by the osseous changes associated with the pathology.

The crista and the fossa do not show correlative degrees of development; a situation which might be explained if the features were due to the effects of different muscle groups. The fossa represents the insertion area of gluteus maximus but the crista, on the medial aspect of the fossa, is largely due to the pull of the pubic fibers of adductor magnus.

Observations on the third trochanter (Table VII) show the greatest number in the "absent" category in the Ancaster and fossil hominids and in the Pongids. In the small sample of Bushmen, however 40% of the femora fell into the "moderate" category. Development of this feature would seem to be correlated, in a loose way, with upward continuation of the linea aspera, the fifth non-metric variable included in this study. As shown in Table VI 45% of the Ancaster specimens show

continuous development of the linea aspera to the base of the greater trochanter; 47% of the same series show either moderate or marked development of the third trochanter. Similarily, 54% show discontinuity in the upward development of the linea aspera; 66% of the same group show either absent or slight development of the third trochanter. The situation is less clear with the Bushmen sample, but the small size of this series may be a factor here. Although the numerical values show that the continuous linea aspera is almost twice as frequent among the males as among the females, the x^2 values do not suggest this difference is significant. This is probably due to the total sample dispersion which shows, for example, that the discontinuous categories are more nearly equal with regard to sex: males = 30% and females = 24%.

It is interesting that when the proximal shaft is preserved in the fossil sample it more often shows a continuous linea aspera than not. The terminal development of the linea aspera in Trinil, Femur I is, as previously suggested, probably a further manifestation of the pathology.

IV.2: RESULTS OF METRIC AND RADIOGRAPHIC EXAMINATION:

Radiographic examination of the internal femoral morphology has been included in this study for several reasons. The first is that such a study involving large samples of both sapient and fossil hominid femora has not been done before. As pointed out in Section II, a number of studies of fossil hominids have included radiographic examinations but in no case have those results been evaluated in terms of the variability in a reasonably large sapient population. Therefore, the observations of earlier workers, while of interest in themselves, were incomplete and are of little value in the scope of wider population studies. Working from such incomplete data, some workers have suggested that certain features of the fossil hominid femur were "archaic" or "imperfectly adapted for bipedal progression". Such suppositions obviously needed to be tested and brought into focus against a large sapient control group. Several workers (Walkoff, 1904; Gorjanovic-Kramberger, 1906; Weidenreich, 1941) have suggested that the cortical thicknesses of the femora of earlier types of hominids were greater than in modern types of man. Therefore, a portion of this work has been directed at examining this hypothesis and the cortical thicknesses at three levels of the femur have been measured on anteroposterior and mediolateral x-rays. Indices

showing the relationship of these diameters to other parameters have also been formed.

Before any secular or phylogenetic implications can be made from these particular parameters and indices it must be determined in what way and to what extent cortical thicknesses are affected by various ontogenetic processes. Considerable work has been done on the relationship between cortical thickness and age of the individual and several studies have been made on bones other than the femur: for example, Rohmann, et al (1967) have studied the ribs, metacarpals and skull bones and Epker and Frost (1966) have studied the V, VI and VII ribs. Rohmann, et al, found that the bones included in their study continued to expand throughout life; Epker and Frost, on the other hand, found that although apposition of new bone continued (as determined through tetracycline labelling *in vivo*) increased endosteal involution resulted in a net cortical loss.

Virtually all studies on the femur have confirmed a gain in the total diameter at mid-shaft with a loss of cortical thickness with increasing age. Atkinson, et al (1962) and van Gervan, et al (1969) found a peak of these effects during the fifth decade of life in females; Smith and Walker (1964) found the peak in the first half

of the seventh decade; Armelagos, et al (1972), on the other hand, found the maximum rates of cortical changes in the pre-menopausal age groups. Trotter, et al, (1967a,b; 1968) found that maximum periosteal expansion occurred during the fourth decade in white females and in the sixth decade in negro females.

The relationship of cortical area to age, is another matter, however. Smith and Walker (1964) reported a continued increase in area throughout life while van Gervan, et al (1969) reported a net loss of cortical area. The figures of Smith and Walker, however, are misleading and were perhaps misunderstood by the authors. Their published figures are for total cross-sectional areas which will take into account the demonstrated periosteal increase with age while ignoring the changes in cortical thickness. By reworking their published data and using their formula, I calculated a net loss of cortical area between their youngest group (45 to 49) and their oldest group (75 to 90) of 12.6%. Although the age groupings are not precisely equivalent this loss is of the same grade as the 9% loss found by van Gervan, et al (1969) between their 32 to 41 age group and their 42 + group.

Trotter and her associates (1967 a,b; 1968) have suggested that the observed changes in periosteal

dimensions may be due to secular changes in populations through time and the apparent effect of "age" may have resulted from the inclusion of more older individuals with earlier birth years in the sample. They therefore tentatively concluded that the transverse diameter of the femur at mid-shaft may be decreasing through time (Trotter, et al, 1968) -- a conclusion in agreement with suggestions made by the previously noted workers.

Whatever the actual effect of aging on bone cortex it is to be doubted that much evidence of these effects will be found in the palaeontologic record. Of the fossil hominid dental remains, a large amount and perhaps the majority, suggests that death did not long follow the eruption of the third molar. Of the period dealt with here, the lower and middle Pleistocene, very few dental specimens showing senile deterioration are known. One may therefore conclude, perhaps, that the physiologic effects of aging have not significantly distorted the picture of human morphology for the period under study here.

Osseous changes in the human femur are also known to have causes other than aging. Osteodystrophies due to renal abnormalities are well known (Vaughn, 1970) and a number of defects in mineral homeostasis are known to affect the femur in radiographically detectable ways.

For example, lack of Vitamin C is known to cause periosteal resorption and cortical thinning (ibid.). Moreover, the occurrance of radiopaque transverse lines in the femoral shaft may also be due to nutritional disturbances or to illness. The transverse lines are at right angles to the long axis of the bone and apparently represent a phase of interrupted or abnormal osteogenesis (Park, 1964). The radiopaque lines were first described by Harris (1933) and the occurrance and etiology of these features have been confirmed by a number of later workers (Acheson, 1959; Park, 1964; McHenry, 1968).

As pointed out in Section II, Koch (1917) has described the proximal and distal trabecular systems in the human femur and his descriptions have been confirmed by radiographic examination of the Ancaster and Bushmen comparative series included in this study.

As described by Koch, the compressive trabeculae were seen to be comprised of two groups: an inferior group ("a") which extends from the medial cortex, in the region of the lesser trochanter, laterally to the area of the greater trochanter and neck and ("b") a superior group which extends from the proximomedial

cortex of the shaft into the articular areas of the head. The tensile trabeculae arise from the lateral aspect of the cortex below the greater trochanter and comprise, according to Koch, three distinct stress systems. The first group ("c") extends in a slightly convex arch proximally from just below the greater trochanter to the superior portion of that trochanter. These trabeculae are slight and are occasionally poorly defined. The major group of tensile trabeculae ("d") begins on the lateral cortex just below the previously described group ("c") and extends upwards, also in an arcuate, convex conformation, to terminate at the inferior portion of the head. It has been suggested by Koch that this group carries the greatest tensile stresses. A third group ("e") begins below both "d" and "c" and extends medially, in a somewhat irregular fashion to end at the medial portion of the shaft and neck. The area of Ward's Triangle usually exists as a space without cancellous tissue in the centre of the neck; the triangle is bounded by systems "a", "b" and "d". A number of the Ancaster specimens did not, however, show a clear demarcation of cancellous tissue in the neck. In these cases, the diffuse appearance of the cancelli seemed mainly due to the lack of orientation in the distal compressive system ("a"). (See Plate VI).

The trabecular systems in the distal shaft and condylar areas are less well defined that those in the proximal portion of the bone; Koch, however, defined several systems of trabeculae for this area. One arises from the anterior cortex, usually beginning just below the shaft mid-point and extending distally to terminate on the posterior articular surface. A second system arises from the posterior cortex at a level similar to the anterior system and terminates at the anterior articular surface. Koch suggested that all the trabeculae "end in lines perpendicular to the joint surface". (ibid.). On the anteroposterior radiographic view both longitudinal and transverse trabecular systems can be seen in the distal femur. The longitudinal system arises from both the medial and lateral cortices and extends distally, parallel with the long axis of the bone, to terminate at the periphery of the condyles. A transverse bracing trabecular system also can be discerned. This arises from both the medial and lateral cortices and extends obliquely, internally and inferiorly, intersecting with the opposing group at apparent right angles. The transverse systems are usually very fine in texture and are poorly defined; in a few specimens in the Ancaster series, however, the oblique lamellae showed remarkable development and extended throughout the distal half of the shaft.

Throughout the Ancaster and Bushmen series the cancellous tissue in the head, proximal neck and distal shaft presented a fine, meshlike appearance; a coarser web of intersecting filaments was seen in the distal portion of the neck and in the proximal shaft. Harris's lines were seen in only three femora in the entire Ancaster series; higher frequencies have, however, been reported for other sapient populations (see especially McHenry, 1968).

Of some interest was the radiographic appearance of the calcar femorale in the Ancaster series; in only eight specimens of the one-hundred included in that group did the appearance of this feature agree with the descriptions given in Gray's and Cunningham's anatomical texts (see below). The usual appearance was one of discrete, thin sheets of lamellar tissue, or merely of longitudinally orientated cancelli, extending from both the proximal and distal cortex into the area interior to the lesser trochanter. In only eight

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" A sheet of compact tissue branches off the posterior wall of the upper end of the cavity and extends upwards, through the spongy tissue under cover of the lesser trochanter, to blend with the compact tissue of the back of the neck; it is called the calcar femorale ... it strengthens the neck" Cunningham's Text Book of Anatomy, 7th Ed. 1937, page 282.

"A thin vertical plate of bone, named the calcar femorale, springs from the compact wall of the shaft in the region of the linea aspera and extends into the spongy tissue of the neck. Medially it is attached to the inner surface of the posterior surface of the posterior wall of the neck of the bone" Gray's Anatomy, 29 Ed., 1946, page 407.

cases did the cancelli join and extend continuously across this area as a "plate".

The statement in Cunningham (op cit) that the calcar femorale serves to "strengthen the neck" would seem open to question. The forces in the inferior aspect of the neck are mainly compressional with a large component of vertical shear stress near the mid axis. As demonstrated mathematically by Culmann (in von Meyer, 1867), Koch (1917) and others and as suggested by the radiographic appearance of the bone in this area, these forces are largely resolved proximal to the area of the lesser trochanter and would seem rather to be related to the resolution of compressive forces in the shaft where the outer layers of cortex have been re-arranged by the activity of psoas major and ilio psoas.

IV.2.i: The Ancaster collection provided an excellent comparative series of nearly complete skeletons with notably little pathology or post mortem damage. As pointed out in Section III.1.i, sexual determinations were made on the pelvis and because of the high reliability of the os coxa for that purpose the sexual differences present in the Ancaster femora are of interest.

The femoral cortex at all levels is considerably thicker in the males than in the females and although the ranges are large and nearly equivalent in both sexes the low standard deviations point out the significance of the mean differences. For example, at the sub-trochanteric level the mean medial cortices are 1.91 mm. different yet the female s.d. is only 1.35 mm. (see Table XV). Similarily, the mean posterior cortices at mid-shaft are also 1.91 mm. different yet the female s.d. is just 1.30 mm. (see Table XVIII). These figures firmly suggest the importance of cortical diameters as a sexually related feature.

Another feature of importance as a sexual selector is the head diameter (see Table XII)- a similar conclusion was reached by Parsons (op cit). The mean female head diameter of 43.02 mm. is just within the

Ancaster male range (42.1 to 53.0 mm.) and the female s.d. of 2.44 suggests the importance of this parameter. All of the remaining parameters of the shaft show large within sex variations and overlapping ranges and are less useful for the purpose of sexual distinction.

The inter-relationships and indeed, possible inter dependence, between certain shaft parameters is suggested by the product-moment correlation coefficients; the relevant data is given in Table XXV. The data quite clearly suggests a highly significant relationship between head diameter, length of the head-neck axis and certain cortical and shaft diameters. The highest correlations in both sexes are between the internal and external parameters at the sub-trochanteric and mid-shaft levels with length of the head-neck axis. Of particular interest are the high correlations in both sexes between the sub-trochanteric medial cortex and transverse diameters and length of the head-neck axis; the additional medial cortical tissue in the upper shaft undoubtedly provides buttressing and stabilization for the high bending moments associated with the longer neck axis. The fact that the lateral diameters are more highly correlated with the length of the head-neck axis at the mid-shaft and sub-pilastric levels could be indicative of the sapient pattern of

weight transmission predominantly along the lateral aspect of the shaft beginning at or above the mid shaft level. This supposition is partly supported by the negative correlation for the sub-pilastric medial cortex and length of the head-neck axis in both sexes. Moreover, reference to Table XVII will show that in the Ancaster sample the lateral cortex exceeds the medial cortex in thickness at the mid shaft level. The Pongids and most fossil hominids, however, show the reverse situation; in the Pongids weight transmission is predominantly along the medial aspect of the shaft.

A final point: in both the Ancaster males and females the length of the head-neck axis shows a high positive correlation with the diameter of the medial cortex at the sub-trochanteric level. However, although the male cortex at this level is thicker than that of the females the coefficient of correlation is less in the males. It would seem reasonable that the larger male cortices are not entirely due to biomechanic necessity and that general male robusticity is a contributory factor in cortical diameters.

In the external shaft indices the Bushmen sample shows little difference from the Ancaster sample in the means.

The clearest differences occur in the proximal area of the bone. The Bushmen mean for head diameter is below both the male and female Ancaster means and the s.d. for the parameter shows that it is not subject to high variation. The mean length of the head-neck axis is also below the Ancaster ranges. The Head/Neck Index shows, however, that these features are relatively very nearly the same in both populations. The cortical indices reveal that the Bushmen shaft is relatively thicker in all orientations at the sub-trochanteric level and in the mediolateral orientation at mid-shaft; anteroposteriorly at mid-shaft the Index is nearly equal with the Ancaster values as is the Index of Cortical Robusticity. Although the Bushmen shaft has relatively thicker walls the cortical dimensions are, in absolute terms, thinner than the Ancaster combined means, except for the posterior cortex at mid-shaft level which exceeds even the Ancaster male mean.

The living Pongids included in this study for comparative purposes were specimens of *Pongo*, *Pan* and *Gorilla*. Since few consistent or significant radiographic variations were found between the members of the different genera all the specimens will be

described within the single category "Pongids".

All trabecular systems present in the Ancaster and Bushmen sample were present in the Pongid sample, the systems differed, however, in their definition and in their relative degree of development. The finely textured, mesh-like appearance of the cancellous tissue in the sapients was not usually seen in the Pongids and the cancellous texture in this group was usually of a coarser nature with larger interstices.

The radiographic appearance of the proximal Pongid femur generally resembles that of the comparative sapient sample. The major compressive and tensile groups ("b" and "d") can be clearly seen to intersect in the femoral head. The tensile trabeculae, especially those in the greater trochanter, are much less well defined than in the sapients of the control groups. This difference, along with the lack of lateral expansion of the greater trochanter, might be explained in terms of varying biomechanical relationships and activities of gluteus medius and minimus in the Pongids and sapients.

Lamellar tissue was never seen to be organized into a discrete plate interior to the lesser trochanter although

some vertical orientation of the cancelli was usually seen in the area. A Ward's Triangle was seen in two Pongid specimens, both *Pongo*. Plate VI shows the clear orientations of the trabeculae and the appearance of a triangular area of diminished radiopacity in the femoral neck of one of these Orangs.

In the proximal shaft spicules of lamellae were frequently seen to project obliquely and inferiorly into the medullary cavity; these appear to intersect at right angles near the longitudinal axis of the bone. Oblique cancelli were occasionally seen in the sapient femora but these were never as large or as radiographically dense as in the Pongids. An explanation may be that with the more distal insertion of gluteus maximus on the Pongid shaft tensile stresses are carried further down the lateral femoral aspect than in the sapients. The resultant sheer stresses would therefore be resolved by these lamellar structures.

Radiographic examination of the distal shaft and condylar areas reveals that while the major longitudinal and transverse trabecular systems are present in the Pongids, as in the sapients, the relative degree of development of each system is more or less reversed in the two groups. The longitudinal systems, so clearly

seen in the sapient femur, are often difficult to identify in the Pongid femur; the transverse cancelli, on the other hand, often very large, extend obliquely and inferiorly into the distal medullary cavity usually beginning about the shaft mid-point.

Measurement of the Pongid x-rays reveals the cortical diameters, in general, to be smaller than the Ancaster means. The greatest differences are seen in the medial and lateral diameters at the sub-trochanteric and mid shaft levels. In the lower shaft, the diameters more closely approach the control means and in a few instances slightly exceed them. The gracility of the proximal shaft is again reflected in the cortical indices for the mediolateral parameters at the upper and mid-shaft levels. In the anteroposterior orientation at the sub-trochanteric level, both *Pan* and *Gorilla* exceed the Ancaster combined means while none exceed it at mid-shaft. The Minimum Breadth Index, which reflects the vertical location of the minimum shaft breadth in relation to total length, also indicates the gracile conformation of the proximal Pongid shaft. Within this group the Index has a mean value of 72 - falling in the upper 1/4 of the shaft - as against a mean of 55 for the Ancaster controls.

The external indices reveal also that the Pongid shaft has a different conformation than the sapient shaft. While generally rounder at the upper end it shows greater transverse diameters at the mid and lower shaft levels; this lateral expansion is particularly marked in the popliteal region where the Popliteal Index is, in all cases, markedly higher than in the controls.

IV.2.ii: RADIOGRAPHIC AND METRIC EXAMINATION OF THE FOSSIL SAMPLE: It has been possible to include ten Upper Pleistocene femora in this study: five from "Classic" Neandertals, two from Oberkassel and three associated with the Rhodesian skull.

Rhodesian: Three femora of Upper Pleistocene age, found in association with the Rhodesian skull will be considered here; a fourth specimen, comprising part of the mid-shaft, is too incomplete for inclusion. Although the three femora are relatively large and robust specimens they are all characterized by having very slight muscular and ligamentous impressions.

Rhodesian 689: In the radiographs of the proximal fragment Ward's Triangle is very poorly defined; this appears to be due to lack of definitive orientation of the inferior compressive system. A small portion of the epiphyseal line is visible radiographically in the inferior portion of the head. The head diameter and the length of the head-neck axis are both above the Ancaster combined means but are within the ranges of that series (see Table XII). The distal fragment is not remarkable radiographically. Externally, both the medial and lateral epicondyles are very large

with the lateral being slightly larger.

The cortical measurements exceed the Ancaster combined means in the upper and lower shaft (with the exception of the lateral diameter at the sub-trochanteric level). At mid-shaft, however, three diameters are more than the Ancaster combined means and the fourth, the anterior diameter, is less. Although the shaft shows absolutely large cortical diameters at the upper shaft, the indices are about equal with the control combined means. At mid-shaft, however, while the diameters are, for the most part, less the indices are approximately equal to the control combined means.

Rhodesian 690: It has not been possible to examine this specimen radiographically; all attempts to obtain x-ray penetration have failed. Superficially, it does not resemble the other specimens; it has a chalky appearance with a very friable surface. The other Rhodesian specimens are very hard, with a rock-like surface, and have yielded good x-rays. The external indices do not differ from the other specimens except for the Platymeric Index which at 67.7, is at the low end of the Ancaster range. It is otherwise unremarkable.

Rhodesian 907: This femur has a remarkably large femoral tubercle at the superior termination of the iliofemoral line and there is a slight degree of osteophyte formation around the superior borders of the head. The head diameter is above the Ancaster male range and the length of the head-neck axis is above the Ancaster female range. Radiographically, Ward's Triangle is more clearly developed than in 689. The external indices of this specimen, as with 689, are entirely within the Ancaster range. The cortical diameters and indices at the sub-trochanteric level, the only ones possible to obtain, show the same pattern as in that specimen with very similar values.

The five "Classic" Neandertal femora included in this study (two from Neandertal, two from Spy and one from Fond-de-Fôret) show a number of features in common: all are characterized by having a large head, long head-neck axis and a markedly bowed shaft; the muscular and ligamentous impressions are always slight. Radiographic examination was possible only in the case of Neandertal. Here, all diameters and indices at the sub-trochanteric level are greater than the Ancaster combined means. At mid-shaft the cortical diameters exceed the control combined means with the exception of the lateral cortical diameter which is less; the

Mediolateral Cortical Index is also less while the Anteroposterior Cortical Index is slightly greater. The degree of bowing (see Table XIV), as indicated by the length of the subtense, is above the range of the Ancaster males but within the range of the females of that group. Reference to Table XXV will show that within the Ancaster group the thickness of the anterior cortex is significantly correlated with the length of the subtense and the anterior cortices in Neandertal exceed the sapient controls at all levels. This would be explicable in terms of resistance to large bending moments set up on the anterior aspect of the shaft by the anteroposterior femoral curvature. The posterior cortices, in the controls, show either very small or negative correlations with the length of the subtense. The head diameters for both Spy and Neandertal are above the range of the controls and the length of the head-neck axis, in Neandertal, is above the control mean but still within that range. In Neandertal, the Head/Neck Index and Neck/Shaft Index, while above the control combined means are within the ranges (see Table XIII).

Oberkassel: Only the Oberkassel male has been examined radiographically; in general the specimen shows similarity with both the Ancaster series and with the Neandertal specimens. The head diameter is above the mean figure

for the male controls and within the male range but above the female range. At the upper and mid-shaft levels the cortical diameters are approximately equal to the Ancaster combined means and usually slightly below the male means; the anterior cortex at the mid shaft and sub-pilastric levels is below the female means. The cortical indices show that the shaft is relatively thinner than the controls in all orientations except anteroposteriorly at mid-shaft. While there is general metric similarity between the Neandertals, Rhodesian and Oberkassel specimens, they differ in that while the former are very slightly marked with muscular and ligamentous impressions, the Oberkassel male is one of the most rugosely marked specimens seen in this study.

Trinil, Femur I: This bone is heavily mineralized but x-ray penetration has, on the whole, been adequate to reveal the internal morphology. The central and distal portions of the neck, however, are an exception and for this reason the distal compressive trabecular system and the area of Ward's Triangle were not visualized. The visible remaining trabecular systems of the proximal end have not been obviously affected by the osteophytic pathology on the medial aspect of the bone and the stress systems appear normally developed.

The osteophyte itself is composed of cortical tissue where it joins the shaft and there is no radiographic evidence of a demarcation between the exostosis and the shaft proper. In the case of the first proximal arch of the exostosis the cortical bone extends ouward for 2 cm. and it is then comprised of cancellous tissue at its margins. In the main body of the exostosis the cortical tissue extends about 1 cm. beyond the assumed former margin of the shaft and the remaining structure is comprised of cancellous tissue. Within the cancellous tissue are numerous, small (averaging less than 1 mm.) radiopacities; they are mainly seen at the margins of the growth. A larger radiopacity, 6 mm. long and presumably a broken drill, is also seen in the exostosis. The medullary cavity at the level of the growth is irregular but not significantly narrowed. Indeed, the cortex shows irregular opacification and uneven borders throughout the entire posterior and medial shaft beginning at approximately the level of the base of the greater trochanter and extending to a point 165 mm. above the condylar plane; the anterior and lateral cortices do not, however, show these features except at the level of the exostosis. The uneveness involves both the medullary and exterior borders of the cortex; the posterior cortex shows irregular thickening throughout the length of the shaft and this thickening continues until the area just superior

to the condyles themselves. In non-pathologic specimens, the cortex generally thins at a considerably higher level and it is possible that this particular condition of the cortex in Trinil I is related to the pathologic processes active in the bone. It is therefore possible that the convex popliteal surface, the subject of much debate in the literature, is due to the pathology and has no taxonomic or functional significance.

A further interesting aspect of the radiographic appearance of Trinil I are linear areas of increased density along the cortico-medullary boundary, extending the entire length of the shaft; this may be due to some post mortem mineralization phenomenon but was not seen elsewhere in this study. The remainder of the shaft is heavily mineralized and reveals virtually no internal structure. As the distal portion of the shaft and the condyles are approached the mineralization diminishes to again allow adequate visualization. Here the longitudinal trabeculae are clearly seen but no transverse systems are visible. The distal articular tissue is unremarkable.

Radiographs of Trinil I have been measured; these measurements, however, must be regarded with a degree of caution in view of the extent of the pathology.

The very large lateral and posterior cortical diameters at the sub-trochanteric level and the large antero-posterior diameter at mid shaft, for example, must not be unduly emphasized. It is fortunate that there exist three other relatively complete femora from Java on which to base a discussion. For these reasons, a metric analysis of this specimen will not be given in detail; the measurements are, however, to be found in the Tables.

Externally, the lateral epicondyle of Trinil I presents a very unusual appearance in that, being compressed anteroposteriorly, it more resembles a crest than the usual rounded tubercle. There is slight osteophyte formation around the distal articular areas, especially on the anterior aspect of the shaft.

Trinil, Femur II: This specimen is also heavily mineralized and only some of the internal structures can be seen. The major compressive and tensile trabecular systems are visible at their area of intersection in the head and a portion of system "c" can be seen in the remaining distal portion of the greater trochanter. A calcar femorale is not visible but vertical orientation of some trabeculae can be seen in this area; adequate visualization is prevented by the degree of

mineralization. The cortico-medullary margins are visible throughout most of the shaft but not in the distal shaft area; no distal cancellous tissue is seen.

With the exception of the anterior and posterior cortical diameters at the sub-trochanteric level, all cortical diameters in the upper and mid-shaft areas are either smaller than or nearly equal to the Ancaster combined means. All measurements at the sub-pilastric level, however, exceed those of the control series. Of the four indices included in this study to demonstrate the cortical thicknesses in relation to total shaft diameter Trinil, Femur II falls below the Ancaster combined means in three; the walls are relatively greater in thickness only at the anteroposterior orientation at the sub-trochanteric level.

Although not determinable with certainity, the preserved parts of this femur suggest that the linea aspera did continue into the base of the greater trochanter. Despite the somewhat gracile appearance of this specimen it was, almost without doubt, a very long bone. At an oblique distance of 400 mm. from the head, the shaft shows no evidence of articular expansion and the estimated total oblique length of 460 mm. must be considered as a minimum.

Trinil, Femur III: This specimen comprises a complete and to radiographic examination, well preserved,shaft but none of the articular areas and none of the proximal trabecular systems are present. Throughout its length, the shaft is unremarkable. At the distal extremity the cortex can be seen to thin and longitudinally orientated trabeculae are present; no transverse systems are visible in this area. Measurement of the x-rays reveals that this specimen is larger in most dimensions than the controls. The posterior cortex at all levels is more than 2 s.d. units above the Ancaster female means and the lateral cortex exceeds the combined means at all levels. The medial cortex at the sub-trochanteric level equals the upper end of the Ancaster female range and the anterior cortex at all levels is nearly equivalent to the Ancaster male means.

Trinil, Femur IV: This specimen is preserved to a degree nearly identical with Femur III but the radiographic appearance of this specimen shows a feature not seen in other fossil hominids in this study. In the medullary cavity of the proximal shaft, to the level of the repaired break, transverse lamina can be seen extending across the canal at right angles to the longitudinal axis of the bone; their appearance is

consistent with "Harris's Lines". Of the nine such lamina present, five extend entirely across the canal; they occur over a vertical distance of 26 mm. and vary from 2 mm. to 5 mm. in distance from each other.

Measurement of the cortical diameters reveals that the cortex is thinner in the posterior and lateral directions at mid-shaft and the posterior diameter at the sub-pilastric level exceeds the control combined mean by only .1 mm. The anterior cortical diameter at the sub-trochanteric level is also smaller than the control combined mean and the indicial relationships of cortical diameter to total shaft diameter reveal that the shaft is relatively thinner than the control male means in the anteroposterior orientation at the sub-trochanteric and mid-shaft levels. In the mediolateral orientation, however, the shaft is relatively thicker at both levels and exceeds the male means in both cases. The external indices all indicate, however, that the shaft is generally flatter at all levels than the Ancaster series.

Peking, Femora I and IV: It is difficult to evaluate properly the internal anatomy of the Peking femora; the radiographs of these specimens included in Weidenreich's 1941 monograph are of poor quality and the specimens are incomplete. Plate XX, in that monograph, of Femur I

reveals tensile lamellae arising from the lateral cortex just below the level of the greater trochanter and compressive lamellae can be discerned radiating from the inferior aspect of the neck.

Weidenreich, working with Walkoff's (op.cit.) definition of only three trabecular systems for the proximal femur, noted three differences between the x-rays of the Peking femora and those of "modern" man. The first of these concerned the way in which the lamellae diverge from the inferior aspect of the neck. Weidenreich stated that Walkoff's Systems I and II (equivalent to Koch's systems "b" and "a" respectively) are not separate and discrete as they are in "modern" man but are "diffuse" and that because of this homogeneous dispersion of the trabeculae Ward's Triangle is absent. These particular arguments are difficult to evaluate because of the nature of the published x-rays but Plate XX, in the 1941 monograph, showing the radiographic appearance of Femur I would seem to support Weidenreich's statements. However, 5% of the Ancaster specimens did not demonstrate a Ward's Triangle radiographically (see PlateVI). Conversely, two specimens (out of a total sample size of three) of the genus *Pongo* did show a Ward's Triangle (Plate VI).

The second difference concerns a trabecular system

beginning on the lateral aspect of the femur which "take (s) a more medial course thus meeting the lamellae on the medial side at an acute angle. The curve of System III is consequently much flatter than in modern man" (Weidenreich, 1941). Here, of course, Weidenreich was hampered by Walkoff's description which recognized only one of the three trabecular systems on the lateral aspect of the femur. What Weidenreich recognized on the x-ray of Femur I was the lowermost of the tensile trabecular systems ("e" in Koch's terminology) which normally follows the pattern Weidenreich described. The main tensile system ("d") is not preserved on the fragment.

Weidenreich's description of the "extraordinary thickness of the walls and the relative narrowness of the medullary canal" (ibid.) is supported by the larger sample used here. All cortical diameters in both Peking femora exceed the Ancaster combined means and except for the posterior cortex at mid-shaft exceed the male means as well. The thickness of the medial cortex at the upper and mid-shaft levels is especially remarkable; Peking I exceeds the female mean at the upper shaft and the male mean at mid-shaft by more than 2 s.d. units. The cortex on the inferior aspect of the neck appears to remain thickened to a more proximal point than in the sapient controls. Although it is not possible to estimate the length of the neck on the two

Peking femora it is possible that such cortical buttressing could act to provide stabilization for a long femoral neck.

The external shaft indices reveal that the Peking femora are flatter anteroposteriorly at all levels and the Minimum Breadth Index shows that the smallest transverse diameter falls lower on the shaft in Femur IV than in the controls. The Minimum Breadth Index of 45 in Femur IV, as oppossed to the Ancaster combined mean of 55, supports Weidenreich's suggestion that the point of least breadth fell low on the Peking specimens.

OH 28: The radiographic appearance and internal preservation of this specimen are not sufficiently good to allow a complete description of its internal structure; the cortex is clearly preserved but virtually no cancellous tissue remains. However, although the lesser trochanter is missing, a very few continuous lamellar plates can be seen immediately interior to the former location of the trochanter; this implies the existence of a calcar femorale although its degree of development cannot be ascertained.

The anterior and posterior cortices are, throughout the length of the shaft, similar to or smaller than the control means; the cortical indices, however, show that

the cortex is, at all levels, thicker relative to total shaft diameters. The medial and lateral cortical diameters generally exceed the control means with the exception of the lateral cortical diameter at mid-shaft which is 0.1 mm. thinner than the combined control mean; as with the Peking femora the differences are most marked in the lateral diameters. The external indices show that the shaft is flatter anteroposteriorly throughout. The Platymeric Index of this specimen, 62, is one of the lowest in the entire series and was below the male Ancaster range. The Minimum Breadth Index of 44 is closely equivalent to the figure for Peking, Femur IV. The linea aspera lies flat on the posterior surface of the shaft without a pilastre, as in KNM ER 803 and the Peking femora. The gluteal markings are clearly defined with a fossa and a crest.

Although the general morphological pattern of this femur is very similar to that of the Peking specimens the slightly smaller cortical diameters, in all but the sub-trochanteric medial and lateral orientations might suggest that it is a female. Day (1971) has suggested that the sexual pattern of the associated os coxa was equivocal but the pattern of these femoral cortical differences between Peking and OH 28, extrapolating from similar data in the control material, is consistent

with the latter specimen being a female.

KNM ER 736: Only the shaft of this specimen remains and therefore none of the proximal or distal cancellous tissue is preserved. On the x-rays, thin lamellar sheets can be seen separating from the internal cortical surface beginning just below mid-shaft; these are orientated in a longitudinal direction and no transverse structures are seen. Towards the distal end of the specimen the cortex thins with a corresponding increase in cancellous tissue but the distal extremity of the shaft is not preserved.

All of the internal measurements of this specimen exceed those of the control means. Moreover, the 2 s.d. range of the Ancaster females is exceeded in the medial and lateral cortical diameters at the sub-trochanteric level and in the anterior and lateral diameters at the sub-pilastric levels. The four cortical indices indicate that the shaft is relatively thicker than the combined control means at the sub-trochanteric level but thinner at the mid-shaft level; the external indices show that the shaft is rounder at all levels than the controls. The hypotrochanteric fossa, without a medial crista, is located lower and more posteriorly on the shaft than is usual in the sapients; the fossa is very well marked. The

posterior aspect of the shaft shows a massive pilastre and the massiveness of this feature is emphasized by the cortical diameters on the posterior shaft. At mid shaft level the cortex is more than 2 s.d. units above the Ancaster male mean and just less than that amount over the "erectus" mean. This specimen is remarkable for the straightness of the shaft. For example, the difference between the minimum shaft breadth and the maximum shaft breadth, at the sub-trochanteric level, is 2.2 mm; in the Ancaster series this difference averages 6.69 mm. and in the "erectus" group 9.6 mm.

At the proximal end of the femoral shaft vertically orientated cancelli can be seen in the region of the lesser trochanter; a clearly defined calcar femorale is not visible, however. Orientation of these cancelli has not been seen in any of the other proximal femora presently attributed to the australopithecine group.

KNM ER 737: This specimen demonstrates fine preservation of its internal structure radiographically, even though much of the neck and all of the distal cancellous tissue are missing. Of primary interest is the great thickness of the cortex throughout the shaft and especially at the inferior aspect of the neck, where the cortex is well preserved. Radiographically, the appearance of the

cortical tissue in the inferior aspect of the neck shows the same thickened, proximal extension seen in the Peking specimens. The medial cortical diameter in the sub-trochanteric region is the largest in this series and the mid-shaft medial cortical diameter is exceeded only by Peking, Femur I; the Minimum Breadth Index is nearly identical to that for Peking. The parameters on this specimen exceed the combined means of the control series in every case except for the posterior cortex at mid-shaft. No trabecular system is preserved although some cancellous tissue remains on the proximolateral aspect and a very slight amount on the medial aspect of the shaft and neck. All of the visible cortical tissue is coarse and shows large interstices; however, sapient cancelli similarily located show similar texture. Spikes of lamellar tissue extend into the proximal medullary cavity orientated in a craniad direction.

An impression for the ilio-femoral ligament is not preserved on this femur; there is a slight elevation on the medial aspect of the neck but this cannot be traced across the anterior surface of the neck because of breakage. The appearance of the linea aspera as a single, sharp line may reflect further activity of the "sand blasting" which has produced a pitted appearance on the rest of the exterior of the specimen both to visual inspection and under

low-power light microscopy. It is possible, due to the height and size of the extant "linea" that there was formerly a pilastre on the posterior shaft surmounted by the linea aspera.

KNM ER 738: The trabecular structures of the head and neck, less the areas of the greater trochanter, are visible on this specimen. Both groups of compressive trabeculae are clearly visible and are well developed. Of the tensile systems only "d" can be discerned. The intersection of the major tensile and compressive systems is clearly seen in the centre of the head and Ward's Triangle is visible. In the area interior to the lesser trochanter a few laminar sheets are visible and a certain amount of vertical orientation of these sheets can be seen. Preservation and visualization are not adequate to determine if, in fact, a calcar femorale did exist. Possible evidence of a healed fracture is seen on the medial aspect of the shaft 3.5 cm. below the repaired post mortem break. The shaft is especially dense radiographically in this area but the precise nature of the cortical tissue structure cannot be clearly seen. Nevertheless, the localized, thickened appearance of the cortex on the original specimen, both internally and externally, is consistent with callus formation over a well-healed fracture. The Poirier's facet is clearly not present on the anterior surface of the neck, as it usually is in the sapients. Although there is some erosion around the superior margins of the head it would seem to have been

located posterior to the coronal plane of the head and neck.

There is some dispute in the literature regarding the significance of this facet (Bertaux, 1891; Pearson and Bell, 1919) but it would seem to represent a slight extension of the capsule on to the neck. An ilio-femoral line is present as is the pectineal line. The gluteal markings on the posterior shaft are very slight and there is no third trochanter. The neck shows considerable anteroposterior compression.

As this is an incomplete specimen showing possible evidence of trauma a complete metric analysis has not been possible. In those measurments which have been possible, for the proximal shaft and articular areas, it is externally a more gracile and lightly constructed bone than those of the control series. The cortical indices, however, show that the cortex is relatively slightly thicker in the sub-trochanteric area in both orientations. These indices and the head and neck parameters are closely equivalent to the data for the Swartkrans femora; this data is given in Tables XII and XIII. While the head diameters of SK 82 and KNM ER 738 are below the Ancaster ranges, SK 97 is containable within the Bushmen range. The head and neck axial length of all

three specimens is below the Ancaster male mean and nearly equivalent to the Ancaster female and Bushmen means. The picture derived from the indices is somewhat different, however. The Head/Neck Index is near the lower end of the sapient control range indicating that the head diameter is smaller, in relation to the total head-neck axial length, than in the sapient controls.

Although the actual length of the neck was not taken in this study, for the reasons expressed in Section III.2.ii, an estimate of "neck" length can be derived from the included data. Using Pearson and Bell's (1919)[1] demonstration of the nearly circular conformity of the sapient femoral head and subtracting the diameter of the head from the total head-neck axial length an estimated "neck" length can be found. These values are given below.

	Head-Neck Length	Head Diameter	"Neck" Length
Ancaster			
Males N=57	78.2 mm.	48.9 mm.	29.3 mm.
Females N=43	68.1	43.0	25.1
Trinil, Femur I	69.9	41.0	28.9
Rhodesian 689	83.1	49.5	33.6
Oberkassel Male L.	77.3	51.9	25.4
Neandertal	82.9	56.2	26.7
KNM ER 738	59.1	34.9	24.2
999	98.0	51.0	47.0
SK 82	69.9	33.8	36.1
SK 97	68.8	37.2	31.6

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1. They found: Vertical Diameter of the Head N=212 46.77 ≠ .13 mm. Horizontal Diameter of the Head N=196 46.38 ≠ .13 mm.

These results reveal that while the estimated "neck" length is longer than the control means for the Swartkrans specimens, KNM ER 738 lies just below the mean for the Ancaster females. Of considerable interest is the very long "neck" length of KNM ER 999, the longest in the entire series.

KNM ER 803: At the sub-trochanteric level the external measurements and the anterior and posterior cortical diameters exceed the Ancaster combined means while the medial and lateral diameters are less. Of the cortical indices only the Anteroposterior Cortical Index at the sub-trochanteric level exceeds the combined control mean; the remaining three indices demonstrate that the shaft is relatively thinner in the mediolateral orientation at the upper and mid-shaft levels. Thus, while this is a broader and flatter femur than the control series the cortical diameters are generally somewhat less; extrapolating from the control data, this would suggest assignation of this femur to a female. The relationship between the medial and lateral cortical diameters at mid-shaft is of interest here; in the entire fossil series and in all of the living Pongids only two specimens show a greater lateral diameter than the medial: KNM ER 803 and Trinil, Femur I. The antithetical situation is found in both sapient control groups where the lateral cortical diameter at mid-shaft shows preponderance over

the medial. The suggested functional significance of this relationship will be discussed in the following section. The external shaft indices indicate that the shaft is slightly flatter throughout than the control series. Although this shaft is quite incomplete the preserved muscle markings are very rugose; the hypotrochanteric fossa and pectineal line show especial development. The linea aspera lies flat on the posterior surface of the shaft without a pilastre; in this it resembles the Peking and OH 28 specimens.

KNM ER 993: This specimen is heavily mineralized and the internal structures are preserved although imperfectly visible in some areas. The proximal articular structures are absent and the proximal shaft, superior to the repaired break at approximately mid-shaft level, is unremarkable. In the distal section, however, extending from the area of the break, it is apparent that fine cancellous tissue fills the medullary cavity. The presence of such tissue has been verified on the x-ray plates and through visual examination of the broken end of the specimen itself, where the cancelli can be seen. Such a condition has not been observed elsewhere in this study. The angle of shaft obliquity of the specimen is difficult to determine since the lateral condyle is heavily eroded but with reasonable reconstruction it would appear to be greater than the 9 to 10 degrees reported by Pearson and Bell (1919) as a mean for their sapient series. The angle of obliquity for this specimen

has been suggested to be approximately 14 degrees (A. Walker, pers. comm.) and my own observations on the original specimen are in agreement with that estimate. This relatively high angle of obliquity would inevitably set up sheer stresses throughout the shaft and this, in line with Koch's hypothesis that such stresses are best resolved by cancellous tissue, might suggest an explanation for this condition.

Metrical analysis shows that while the cortex is very thick both relatively and absolutely at the sub-trochanteric level it is thinner than the controls at the mid shaft and sub-pilastric levels; the Robusticity Index for mid-shaft is thus slightly below the Ancaster combined mean. Other indices and the external parameters are very close to the control means.

This specimen has been attributed to *Australopithecus* (Leakey, 1972) but such a relationship is not fully substantiated in the metric analysis and the position of this specimen in the multivariate analyses (see Section IV.3) suggests considerable biometric distance from that group. The only metric comparisons which can be made with other australopithecines in the proximal shaft show that KNM ER 993 has much thicker cortices in the medial, anterior and posterior orientations at the

sub-trochanteric level than the Swartkrans femora and KNM ER 738. The comparative data for the distal femora is presented in Table XI and below. From this data it can be seen that the shaft and bicondylar widths are absolutely larger in KNM ER 993 but the other condylar parameters do not conclusively separate the east African specimen from the South African material.

	Bicondylar Width	Max. Length Ext. Condyle	Max. Length Int. Condyle
Ancaster			
Males = 57	78.7 mm	62.5 mm	56.5 mm
Females = 43	70.4	62.1	55.7
Bushmen = 8	67.5	57.9	57.1
Pan = 3	69.3	43.4	51.5
Gorilla = 3	83.1	61.2	52.7
Pongo = 3	50.2	33.5	41.7
Spy 8	85.3		
Neandertal R.	87.6		
L.	88.8	72.1	67.9
Rhodesian 689	83.1	70.8	64.2
Trinil, Femur I	76.1	60.1	58.5
Omo	75.9	60.9	63.1
KNM ER 993	61.3		40.5
999			
TM 1513	53.4	41.6	41.1
STS 34	56.3	43.8	

	Shaft ML [1]	Shaft AP
KNM ER 993	38.4 mm	27.4 mm
TM 1513	31.9 [2]	20.2
STS 34	32.4 [2]	23.1

The intercondyloid notch shows an imprint for the origin of the posterior cruciate ligament and a small

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1. These shaft dimensions were taken at 2 cm. above the anterior superior articular margin of the external condyle.
2. These measurements were taken on casts.

portion of the groove for popliteus is present on the lateral condyle. A valgus position of the knee is indicated by the strong development of a lateral buttress on the patellar surface to prevent lateral dislocation of the patella.

KNM ER 993 shows a marked amount of anterior shaft bowing yet the anterior cortices at the mid-shaft and sub-pilastric levels are below the Ancaster female means.

This is an unexpected situation in view of the high correlation coefficient between these diameters and shaft bowing found in the controls; this condition might suggest that the biomechanic stresses, particularly of a tensile nature, on the anterior shaft, below the sub trochanteric level, were not resolved in the same way as in the controls. Specifically, if the centre of gravity were located anterior to the hip joint then the highly bowed shaft of this specimen would have been subjected to less anteroposterior bending moments than in a comparably shaped sapient femur, hence necessitating less cortical mass for resistance. Such an anterior location of the centre of gravity has been suggested for OH 20 by Day (1969a), using other morphologic criteria.

KNM ER 999: This is a virtually complete specimen lacking only a very small portion of the distal shaft just proximal to the condyles and the anterior surface of the distal shaft; part of the lateral condyle is also missing. The bone is remarkable for its length which is outisde the Ancaster range (Ancaster males = 342 mm. to 420 mm.). The shaft length, as taken for this study, is estimated at 466 mm; based on the reconstruction formula discussed previously (see Section III.2.i) the total oblique length would have been approximately 491 mm. The centre of the head is preserved but the margins are eroded; the point where the head

joins the neck is present on the anterior shaft and based on the assumption that the femoral head is symmetrical, or nearly so, (Pearson and Bell, 1919) the head diameter has been taken horizontally on the x-rays from the preserved portion at the centre of the articular surface to this point on the neck. The head diameter is outside the range of the Ancaster females but within the male range. The length of the head-neck axis and "neck" are both the largest in the entire series. Both a hypotrochanteric crista and fossa are present; a third trochanter is not present and the linea is discontinuous. A marked pilastre is present on the posterior shaft.

All of the external measurements exceed the control combined means but despite this the bone is not robust internally. The anterior cortex at the sub-trochanteric level and the medial and lateral cortices at mid-shaft are all less than the Ancaster combined means and all of the cortical indices are below those means. In view of the relative thinnesss of the shaft walls the possibility that the bone has suffered sufficient weathering, internally and/or externally, to reduce the cortical diameters shouls be examined. Externally, with low powered light microscopy the cortical tissue shows slight damage but this does not seem excessive since the

external markings of the upper shaft are very clear and sharp; internally the x-rays show part of the main compressive trabecular system in the head and neck. It must, therefore, be assumed that the measurements are not artifacts of preservation and represent fairly accurately the true morphology of the bone.

SK 82, SK 97: These two femora from Swartkrans are sufficiently similar to be discussed together. On the anteroposterior radiographic view the cancellous tissue is clearly seen to be preserved. The textural appearance of this tissue, fine in the head with a coarser web in the neck and proximal shaft, is similar to that seen in the sapient controls. Of the compressive systems "a" can only be slightly seen but the main system, "b", is clearly visible. Of the trabeculae arising from the lateral aspect of the proximal cortex, the major tensile arch "d" is plainly visible and can be seen to intersect with "b" and Ward's Triangle is present. The orientation and development of these trabeculae does not apparently differ from the sapient series. It is possible however, that the tensile system in the greater trochanter ("c") was not as well developed in these individuals as it is in the sapients. Although this system is occasionally poorly defined in the modern sample some degree of orientation is nearly always seen. In SK 82, however,

the clearly visualized cancellous tissue of the greater trochanter shows no directional orientation; it is possible that in SK 97 the tensile system "c" shows a slight degree of development although the orientation and radiographic density are still weak. In both specimens the greater trochanter lacks the lateral flare typical of the sapients and this, along with the evidence of the radiographs might be used to support the suggestion that the pelvic stabilizing mechanisms were less efficient or functioned differently in these early hominids than in modern man. The radiographic evidence suggests that tensile stresses on the greater trochanter were different than those stresses in modern man. Also of interest on these x-rays is the complete absence of laminar orientation in the area of the lesser trochanter. The cancellous tissue, well preserved in the fossils, lacks any clear organization or orientation and in this more closely resembles the radiographic appearance of the Pongid femur than the hominid. The lesser trochanter appears to be more laterally placed than in the sapients. The metric evidence shows that the parameters of the upper shaft were both relatively and absolutely larger than the control series. The parameters of the head and neck have been discussed previously. The neck is flattened anteroposteriorly in both specimens and the Poirier's facet is placed posterior to the coronal plane of the neck. On the posterior aspect of the neck a groove is

present in both specimens for the obturator externus tendon; the presence of this groove is strongly indicative of full extension or hyperextension of the hip.

Because of their incompleteness, the following specimens have not been included in the complete metric study.

OH 20: This very small fragment could not be included in the larger study; good x-rays are available, however, and are of interest. The specimen including only the proximal shaft and most of the neck shows well preserved cancellous tissue throughout; this tissue is very fine in texture. Both compressive systems are preserved but do not appear well defined. The major tensile arch "d" is seen at its origin at the top of the greater trochanter and the lower tensile system "e" is also seen in the proximal portion of the shaft. The appearance of the cancellous tissue within the greater trochanter is very like that described for SK 82; the tissue lacks orientation and no orientated trabecular structure can be seen; Ward's Triangle is apparently not present due to the lack of definite orientation of the lower compressive system. The greater trochanter again lacks lateral flare and the neck is flattened anteroposteriorly. A distinct ridge for ilio-psoas extends distally below

the lesser trochanter. A groove for obturator externus is present; the insertion area of the ilio-femoral ligament is smooth.

KNM ER 815: Although this specimen is very incomplete and almost entirely radiopaque its external appearance is of interest. The only index possible to obtain, the Platymeric Index, has a value of 70.5 and although this indicates a somewhat flattened shaft it is not remarkable. The base of the greater trochanter shows that the specimen could not have had the lateral flare of the sapient type. The proximal muscle markings are very slight but there may be a slight ridge for ilio-psoas extending below the lesser trochanter. The existence of a groove for obturator externus cannot be determined; the femoral neck again shows considerable anteroposterior flattening.

IV.3: STATISTICAL RESULTS: The data considered in this study was comprised of 134 specimens, 17 of which were fossil femora; 44 variables were used for the most complete specimens. While visual and metric examination of the material provided detailed and particulate information such examination could provide very little information about wider patterns of morphology and relationships. For the purpose of defining metric patterns of morphology and biometric relationships multivariate statistical approaches have been demonstrated to have considerable applicability and reliability in the past (see Section III.3). The multivariate method used here, a discriminant function analysis which incorporates Mahalanobis' D^2 statistic and canonical analysis, is available as the BMD 07M program and was run on the CDC 6600 and 7600 computers at the University of London Computer Centre.

The main problems encountered in such an evaluation are due to the incompleteness of the fossil material. For example, the measurements of the head and neck seem to be of very high discriminatory value for the early lower Pleistocene hominids of east and South Africa yet only one complete (Trinil, Femur I) and two very eroded heads (Trinil, Femur II and KNM ER 999) of late lower or middle Pleistocene age exist. Similarily, differences in the mid and lower shaft seem to be of useful discriminatory

value in separating middle Pleistocene and later hominids yet it is the proximal shaft which is most often preserved in the lower Pleistocene hominids. Therefore, the major difficulty in a multivariate examination of the total sample is the selection of those parameters which have high discriminatory value and are preserved in a maximum number of specimens. In evaluating the entire series, the most satisfactory, indeed the only, solution was the use of parameters from the sub-trochanteric and mid-shaft areas only. By removing certain very incomplete specimens from the sample parameters of the lower shaft could be considered as well. Effectively, this meant that the australopithecine femora, from Swartkrans, and KNM ER 738 were removed from the calculations. This also meant, however, that a maximum number of parameters, including those of the lower shaft, could be compared on the more completely preserved femora of middle Pleistocene age.

A further problem encountered in the use of a discriminant function analysis is the necessity of dividing the fossil material into groups before statistical evaluation. Construction of the final groups was based on a combination of visual, metrical and multivariate analyses. The primary "erectus"[1] group was comprised of Peking, Femora I and IV and OH 28. This grouping seemed secure because of the

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1. This term is placed in quotation marks because it is not intended as a taxonomic term; it is used, for present purposes, strictly as a convenient name.

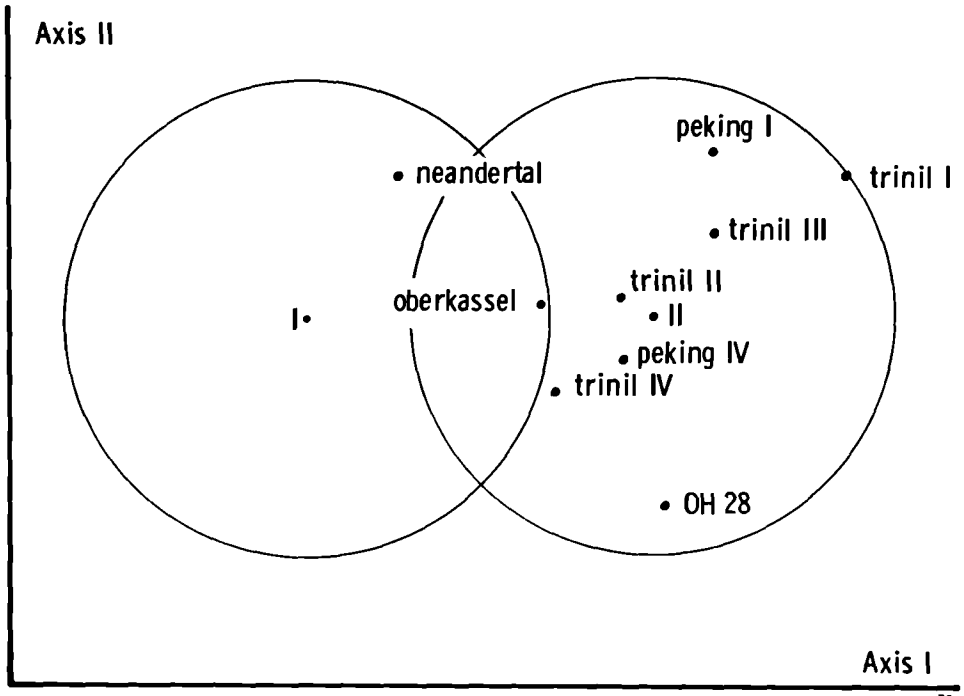
very close morphological similarity of these specimens. Using the BMD 07M program the four Trinil femora were interpolated into the canonical space occupied by the Ancaster and "erectus" populations. Diagram I shows the results of this analysis, which used 27 variables of the internal and external shaft. While 8% of the Ancaster specimens and Oberkassel were included within the "erectus" space none of the Trinil femora encroached on the sapient space.

Diagram I also shows that dispersion is only on the first canonical axis and the mean coordinates for the second axis are -.00 for both groups. The indicated dispersion is due to the greater broadness and flatness of the "erectus" shaft at the upper and mid-shaft levels. The D^2 values for this analysis are given below; while demonstrating that the Trinil femora have greater biometric affinity with the "erectus" group they also suggest that none of the middle Pleistocene specimens has a large distance from the Ancaster means.

	Distance (D^2) from Ancaster	Post. Prob. for inclusion in group.
Peking, Femur IV	31.289	.062
Trinil, Femur I	48.593	.000
Trinil, Femur II	20.060	.044
Trinil, Femur III	15.450	.352
Trinil, Femur IV	25.523	.016
OH 28	21.996	.006

diagram I

CANONICAL VARIABLES I, II



I = Hs - Ancaster
- Oberkassel
- Neandertal

II = He - Peking I, IV
- OH 28

27 Variables of the Upper, Mid & Sub- Pilastric shaft.
radius = 2 S.D.

Hs - Homo sapiens

He- Homo'erectus'

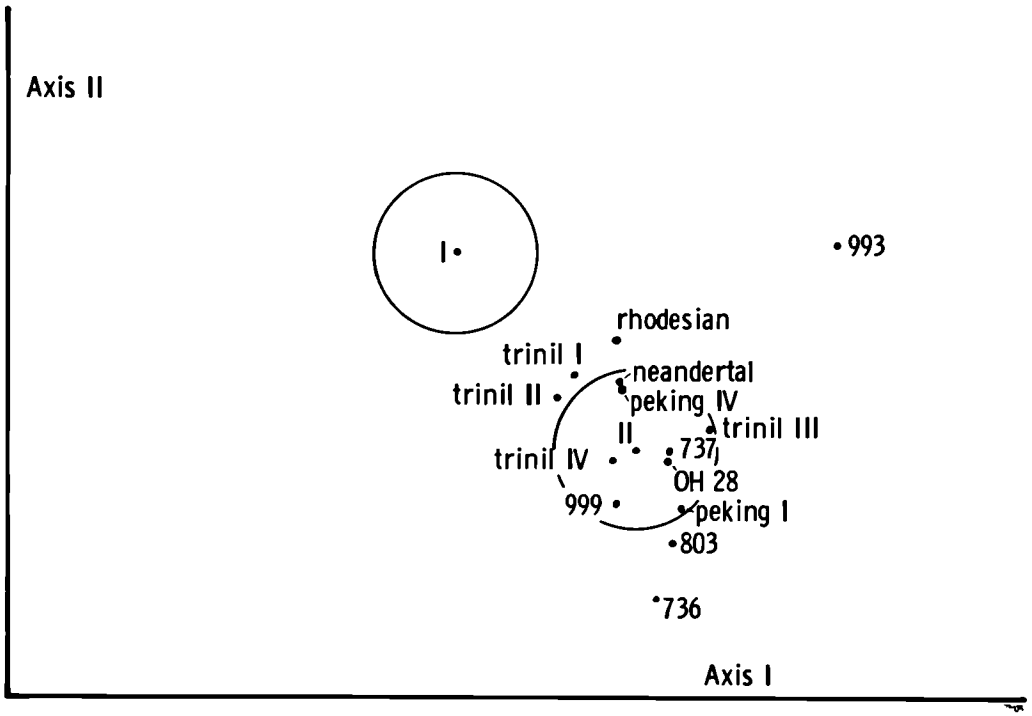
	Distance (D^2) from "erectus"	Post. Prob. for inclusion in group.
Peking, Femur IV	25.845	.938
Trinil, Femur I	30.902	1.000
Trinil, Femur II	13.885	.956
Trinil, Femur III	14.231	.648
Trinil, Femur IV	17.301	.984
OH 28	11.834	.994

Although these D^2 values do not indicate great biometric distance between these specimens the probability figures approach unity for all but Trinil, Femur III for inclusion into "erectus".

The recovery of new hominid femora from the Koobi Fora and Ileret areas of East Rudolf added further specimens to the study sample. Using the Ancaster group, expanded by the addition of Bushmen femora, and the "erectus" group, KNM ER 736,737, 803, 993 and 999 were interpolated into that hyperspace. The results are given in Diagram II. The Swartkrans femora and KNM ER 738 were not included in this analysis because of the use here of mid and lower shaft parameters, as well as the upper shaft values. Dispersion along the first canonical axis is due mainly to the larger upper and mid-shaft parameters in the "erectus" group. Parameters in the medial, lateral and transverse orientations at these levels were especially contributory. The dispersion on the second canonical axis is due primarily to the smaller

diagram II

CANONICAL VARIABLES I, II



I = Hs - Ancaster
- Bushmen
- Neandertal

II = He - Trinil I-IV
- Peking I-IV
- OH 28

Radius = 2S.D.

27 Variables of Upper, Mid & Sub-Pilastric shaft.

parameters at the sub-pilastric level in the "erectus" group, again especially in the medial, lateral and transverse orientations. KNM ER 737 fell close to OH 28 and the "erectus" mean coordinates; KNM ER 736 fell approximately 4.5 s.d. units from that mean; KNM ER 803 fell $_{2.3}$ s.d. units, KNM ER 993 fell approximately 7.0 s.d. units and KNM ER 999 fell less than 2 s.d. units from the "erectus" mean coordinates. The D^2 values and the posterior probability figures for this analysis are given below.

	Distance (D^2) from Ancaster	Post. Prob. for Inclusion in group.
KNM ER 736	458.673	.000
737	120.221	.000
803	190.986	.000
993	170.016	.000
999	167.581	.000

	Distance (D^2) from "erectus"	Post. Prob. for Inclusion in group.
KNM ER 736	339.567	1.000
737	49.366	1.000
803	95.676	1.000
993	118.932	1.000
999	93.290	1.000

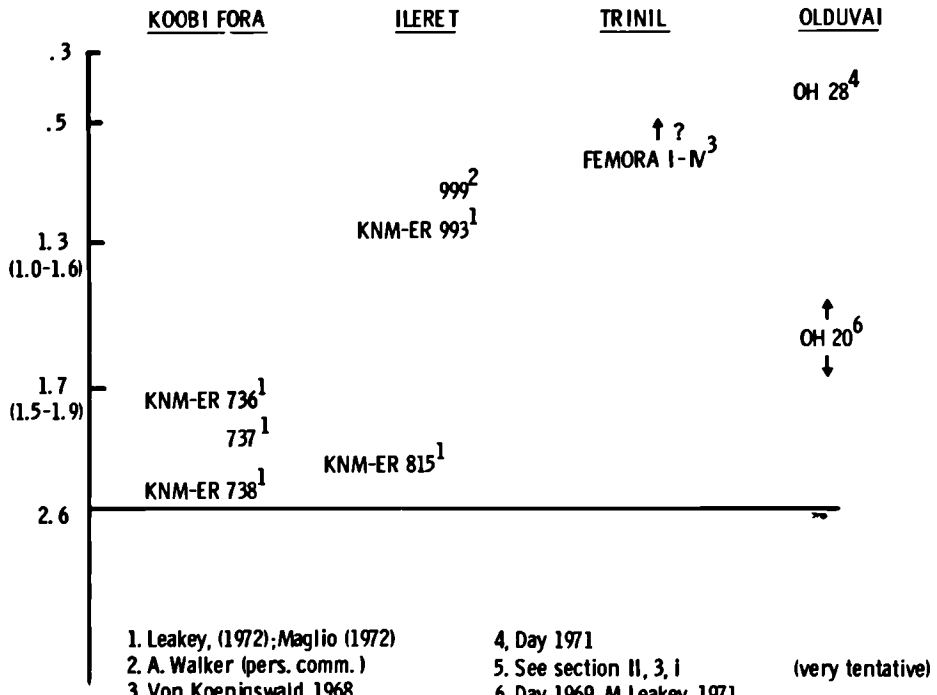
Thus, on the basis of their position in the canonical space, the D^2 values and the posterior probabilities, KNM ER 736, 737, 803 and 999 can be included confidently, in a statistical sense, in the "erectus" space. The positions of KNM ER 736 and 993, while still statistically

included within that space are slightly less clear in view of their large biometric distance from the other specimens and groups; this position is made more interesting because of the near contemporaneity of KNM ER 736 with KNM ER 737 and 803 (see Diagram III). Although the analysis has classified both KNM ER 736 and 993 into "erectus" one of the difficulties with any program based on a discriminant function is that the specimens can only be placed in the *a priori* groups made available and the possibility that the specimens belong to a yet undefined group is not included in the calculations. Nevertheless, the apparent hyperspatial proximity of KNM ER 736 and 803, as seen in Diagram II, is perhaps significant in view of their temporal and geographic proximity.

In order to possibly clarify the equivocal position of KNM ER 736 and 993 and to further develop the hyperspatial relationshps between the hominids a number of pongid femora were introduced into the program; the results of this analysis are given in Diagram IV. On the basis of the results recorded in Diagram II, KNM ER 737, 803 and 999 were added to the "erectus" group. On the first canonical axis those parameters now producing the greatest separation are those at the sub

diagram III

TEMPORAL POSITIONS :
LOWER & MIDDLE PLEISTOCENE HOMINIDAE

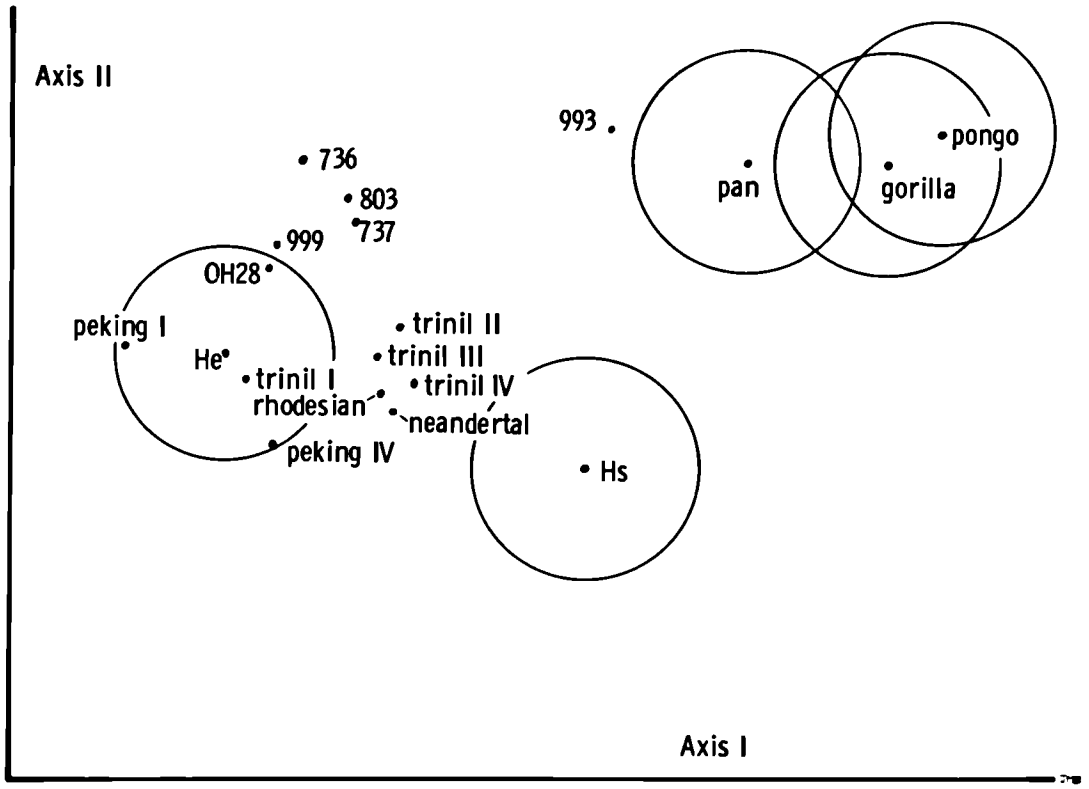


1. Leakey, (1972); Maglio (1972)
2. A. Walker (pers. comm.)
3. Von Koenigswald, 1968
(Based assumed contemporaneity)
4. Day 1971
5. See section II, 3, I
6. Day 1969. M. Leakey 1971

(very tentative)

diagram IV

I, II CANONICAL VARIABLES



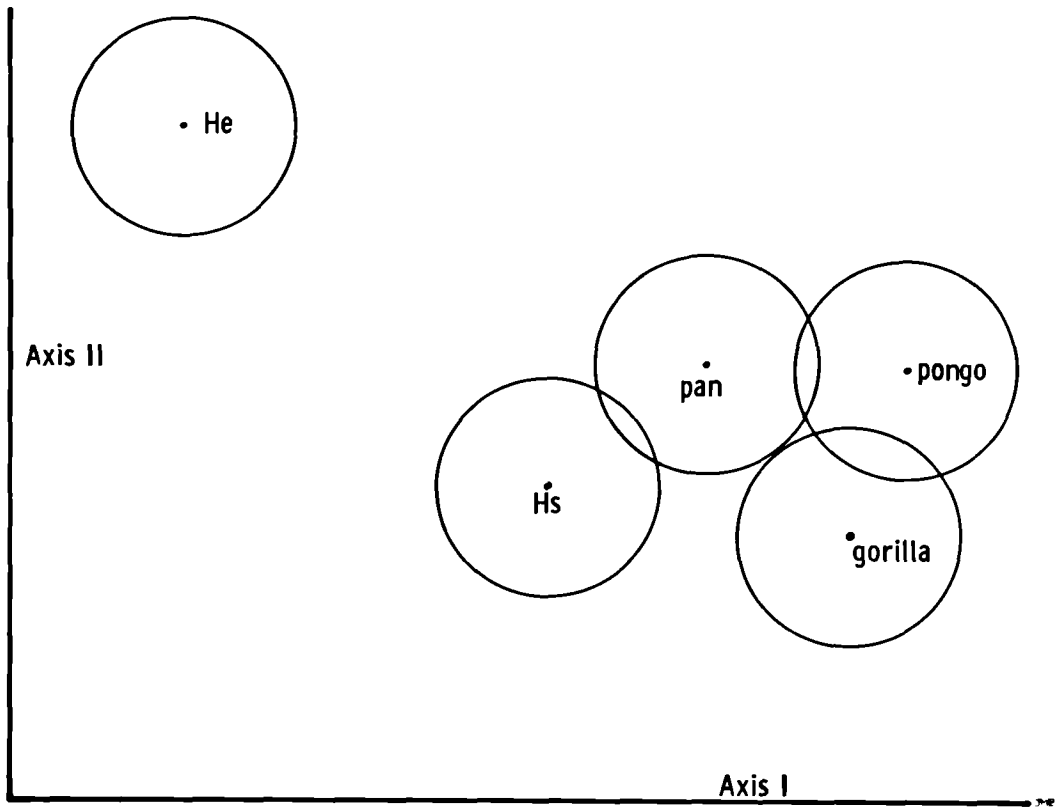
35 Variables & Indices of Upper, Mid & Sub Pilastric shaft

Radius =2S.D. 1st, 2nd Canonical Variables

Ancaster	- Hs	Peking	- He
Bushmen	-	OH28	-
Neandertal	-	737	-
Oberkassel	-	803	-
		999	-

diagram V

CANONICAL VARIABLES I, III



Variables & Groups as for diagram IV
radius = 2 S.D. 1st;3rd Canonical Variables

Co-ordinates for the III axis were given only for groups; Individuals could not therefore be plotted.

trochanteric level; the "erectus" specimens having the highest values here, especially in the medial and lateral orientations and the pongids the least. On the second canonical axis it is parameters at the mid and sub-pilastric levels which are the most discriminatory. Although the shaft is relatively thicker in "erectus" at both levels the external indices place that group in an intermediate position between the pongids and sapients with the pongids having the highest Pilastric and Sub-Pilastric Indices. The very small cortical diameters in the pongids in the medial and lateral orientations at the sub-trochanteric and mid-shaft levels also have been contributory to this dispersion. Reference to Diagram V, which shows the dispersion along the first and third canonical axis, demonstrates that the pongids and the sapients are more closely spaced than on the first two axes. This pattern of dispersion is due largely to the sub-pilastric cortical diameters which are very similar in these two groups with the "erectus" having higher values. Thus on the first and third axes the distance between the sapients and "erectus" is 8.8 s.d. units while the first two axes show this distance to be only 6.7 s.d. units.

Perhaps the most interesting feature of Diagram IV is the placement of the Trinil specimens, along with

Neandertal, in a position somewhat intermediate between the sapient and "erectus" populations; a somewhat similar situation will be found in Diagram II. This development occurred for two reasons. First, the addition of the pongids helped to develop the canonical space and thus the relative positions between the specimens could be defined more accurately. Secondly, this analysis included a number of additional parameters in the form of indices taken from both internal and external measurements and this undoubtedly helped to develop the dispersion between the groups and individuals. As a group, the Trinil femora, Rhodesian, Neandertal and Oberkassel fall fairly closely to the second canonical axis of the "erectus" group but are much more separated from both "erectus" and the sapients along the first axis. The conformation to the second axis is due mainly to the similarity of the mid and lower shaft between "erectus" and the Trinil-Rhodesian-Neandertal-Oberkassel group which are greater than the sapient combined means in most cases. The real metric intermediacy of the group appears at the upper shaft and although there is considerable variability in the individual parameters of these specimens the cortical measurements and indices at the sub-trochanteric level generally fall somewhat between the "erectus" and Ancaster combined means.

Table XXIV gives the D^2 values for this analysis. Trinil, Femur I falls approximately equidistant between the sapient and "erectus" groups but the remaining Trinil femora and Neandertal fall closer to the sapients. These values, however, reinforce the-biometric intermediacy of the Trinil and Neandertal femora.

Of further interest in these figures is the demonstration of the relative biometric proximity of the pongid sample with the Ancaster sample. This closeness occurred because of the relative and absolute thinness of the pongid femoral cortex. In virtually all cortical parameters and indices the pongid femora are equivalent to or thinner than the control means and this clearly maximizes their biometric distance from the thicker "erectus" group.

Table XXIV also reveals a major interpretative difficulty with the D^2 statistic. While the biometric distance of the specimen from a comparative group can be determined it is not possible to describe the direction of that distance since "direction" in a hyperspace is meaningless. Thus, although KNM ER 737 and the gorillas have the same D^2 distance from Ancaster it would not be reasonable to suggest that they belong to the same taxonomic or morphologic group.

It is for this reason that multivariate statistics, while contributing valid and useful insights into the material at hand must not be expected, nor indeed allowed, to formulate supposedly complete answers to questions of biomechanical or taxonomic affinity.

The final analysis including all of the specimens in this study was made; due to the incompleteness of many specimens only 19 parameters of the upper and mid shaft could be used. An "australopithecine" [1] group was included in the calculations for the first time. In the construction of this group features of the head and neck clearly set SK 82, SK 97 and KNM ER 738 together (see Section IV.2). KNM ER 993 was included with this group because of some similarities of its distal shaft and articular areas with TM 1513 and STS 34 (see Section IV.2).

The D^2 values, recorded in Table XXVII, again show Trinil, Femur I equidistant from both the sapient and "erectus" groups. Trinil, Femur III also falls approximately mid-way between these groups and Femora II and IV show greater biometric affinity with "erectus". The posterior probabilities show that all but Femur I should confidently be placed with "erectus"; in the

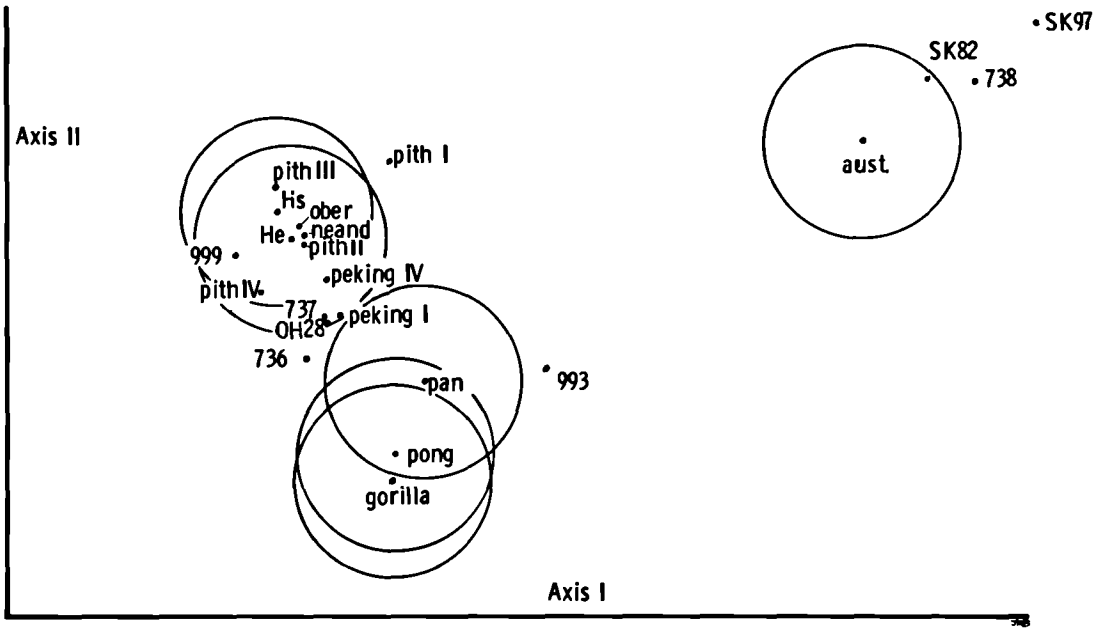
1. This term is used only as a name here and is not intended as a taxonomic attribution.

case of Femur I the probabilities are only slightly weighted in favor of attribution to the sapient group. On the basis of the proximal shaft parameters KNM ER 737, 803 and 999 and OH 28 are again confidently included in "erectus"; the affinity of KNM ER 736 with the "erectus" group is again reaffirmed as is its greater biometric distance from the "australopithecines". SK 82, SK 97 and KNM ER 738 again form a cohesive group.

Diagram VI records the results of the canonical analysis of this data and demonstrates that the proximal shaft is less discriminatory for separating the later hominids than is the shaft as a whole. On the basis of this data the sapient controls and the "erectus" mean canonical variables are 0.80 s.d. units distant. The "australopithecine" mean is approximately equidistant from both the sapient and "erectus" means (11.90 and 11.75 s.d. units respectively). As in the other analyses, KNM ER 993 has fallen relatively close to the "erectus" mean, here 5.75 s.d. units from "erectus" and 6.60 s.d. units from the sapients. Similarily, KNM ER 736 has also fallen closer to the "erectus" mean than to the "australopithecine" group

diagram VI

CANONICAL VARIABLES I, II



1 Radius = 2S.D.
19 Variables: Sub-trochanteric& mid shaft

Ancaster - Hs
Bushmen -
Neandertal -
Oberkassel -

Peking - He
Trinil -
OH 28 -
KNM 737 -
803 -
999 -

SK 82 - Aust
97 -
KNM-ER738 -
993 -

to which both of these specimens have been attributed. KNM ER 736 has fallen 2.45 s.d. units from the "erectus" mean, 3 s.d. units from the sapient mean but 12.25 s.d. units from the "australopithecines".

These D^2 values demonstrate the minimal discriminatory value of using only the upper and mid-shaft parameters for the later hominid specimens. Thus, although the upper shaft parameters are demonstrably different between the sapient and "erectus" groups, the significance of these differences becomes more apparent when they are considered as part of a larger metric pattern: i.e. the total shaft. Moreover, on this analysis ten Ancaster specimens and Neandertal classified as "erectus" and one Ancaster classified as *Pan*. Of interest, however, is the suggestion from this analysis that while the upper and mid-shaft values have not changed to a large extent among the later hominids very remarkable differences exist between the "australopithecine" group and the later specimens.

Table XXVI gives the means for the sapient groups and, where possible, for the fossil groups composed according to the results discussed in this section. The validity of these means is indicated by the size of the standard deviations. In many parameters, the standard deviations

for the fossil sample are below the values for Ancaster. The Platymeric Index, the subject of much discussion in the literature as a "primitive character" is virtually the same for the Ancaster combined group, "erectus" and the "australopithecines": 78.76;78.83 and 78.90 respectively. However, although the external parameters have remained virtually unchanged in the three groups through time significant internal changes have occurred in the upper shaft; these changes are most clearly reflected in the cortical indices for the sub-trochanteric level. Thus, in the mediolateral orientation the Ancaster combined mean of 44.23 is considerably less than the "erectus" mean of 49.88 and the "australopithecine" mean of 53.72. A similar pattern emerges in the anteroposterior orientation at that level with means of 39.24 and 48.32 for the Ancaster combined group and "erectus" respectively. The "australopithecine" mean in this orientation, 43.26, seems to be part of a biomechanical structure which is characterized by strong medial and lateral buttressing and slight anteroposterior stressing.

The differences are less marked at mid-shaft between the "erectus" and sapient groups although the strong mediolateral buttressing persists in the "erectus" group the anteroposterior cortices are here relatively thinner. The strong mediolateral buttressing in "erectus" is

demonstrated not only in the higher cortical index in this orientation but in the larger mean transverse shaft diameter, 29.93 mm, as oppossed to 26.91 mm for the combined Ancaster group and in the lower Pilastric Index in "erectus".

At the sub-pilastric level the "erectus" shaft is slightly smaller than the sapients but the cortical diameters are again generally slightly greater. The only exception is the posterior cortex at this level which is .01 smaller in "erectus" than in the Ancaster combined group. The smaller lower shaft in "erectus" is also reflected in the Minimum Breadth Index.

It is seldom possible to obtain the Popliteal Index in fossil hominids but in those specimens where it is preserved it suggests a somewhat rounder shaft at this level than in the controls. Thus, Peking, Femur IV has a Popliteal Index of 96.1, Trinil, Femur I, 88.9 and Trinil, Femur II, 108.0, as opposed to the Ancaster combined mean of 73.21. The "australopithecine" specimens, STS 34, TM 1513 and KNM ER 993 fall very close to the Ancaster mean.

V.1: CONCLUSIONS: The purpose of this investigation has been twofold. First, to analyze the hominid femur through a variety of techniques with the purpose of recognizing and defining any changes in the morphology and functional anatomy of that bone through the Pleistocene. Second, has been the exploration of the significance of these changes for the taxonomic or classificatory category of the population from which they were derived.

The data presented suggests the coexistence of two types of hominid femora in the lower and early middle Pleistocene. These types were contemporaneous for a period of unknown duration but new and unreported femora from East Rudolf suggest that the types were locally coexistent as early as perhaps 3 million years ago (Leakey, in press); however, determination of the terminal date of that coexistence is not yet possible. For convenience of reference the types will be referred to as "hominine" and "australopithecine"; these are semantic devices and are not intended as classificatory attributions.

The radiological, metrical and anatomical evidence suggests that both types habitually moved in an erect and bipedal mode and there is evidence that the "australopithecine" limb was capable of full extension at hip and

knee. Because of the contemporaneity of the two types the question must be considered whether these types represent ancestor-descendant populations or whether they are only very distantly related hominids showing independent and parallel evolutionary trends toward bipedalism. I suggest that the answer lies between the two possibilities. Contemporaneity does not obviate the possibility that a single nuclear population diverged ethologically, geographically and/or genetically at an early date giving rise to two highly adapted sub-populations which then continued to develop similar locomotor adaptations. These populations then followed genetically separate but similar evolutionary paths each demonstrating erect bipedalism achieved through a slightly different morphological complex. The significance of the apparently long term contemporaneity of these types must not be under-emphasized. The continued local coexistence, and implied successful competition, of the two hominids clearly indicates the high level of adaptation achieved by each.

It is further apparent from the material in hand that there was no morphological variation of functional significance within the known "australopithecine"

femora. Size differences occur, it is true, but the basic morphological complex remains the same. Although the cranial and dental material attributed to this group shows very wide variability of disputed taxonomic significance this variability is not reflected in the anatomy of the femur.

It should be recognized that the degree of relationship between the two types is not known at present but the large biometric distance between them, without known intermediates, suggests the possibility that the "australopithecine" femoral type, as exemplified by SK 82, SK 97, TM 1513, STS 34, OH 20 and KNM ER 738 and 815 may not be fully representative of the ancestral femoral type and may represent a somewhat specialized side branch.

Whether or not we are dealing with an ancestor-descendant population the control femora differ in several ways from all of the fossil hominid material included in this study. The features involved show internal biomechanical relationships and significant mathematical correlations. First, it is clear that the cortex of the hominid femur has become thinner with time. Although cortical thicknesses are, in the control group, somewhat related to sex reference to the Tables

will show that in most cortical diameters "erectus" and (at the sub-trochanteric level) the "australopithecines" exceed the means for the Ancaster males. The values from the correlation matrices suggest, moreover, that cortical diameters are intricately interwoven with other femoral characters. It has been shown that cortical thickness and shaft diameters at many levels and orientations on the shaft (see Section IV.2) are highly correlated with the length of the head-neck axis. It is therefore apparent that the long axis is relatively inefficient in terms of weight transmission and requires greater cortical mass to resolve the compressive stresses set up by the long lever arm. It is also apparent that the length of the head-neck axis is related to the Minimum Breadth Index in the controls. The correlation data (see Table XXV) suggests that the longer the axis the lower the point of minimum breadth on the shaft.

Drawing these two anatomical factors together - the high correlation of the length of the head-neck axis with certain cortical diameters and a low point of minimum shaft breadth - it may be hypothesized that the "erectus" femora which possesses both thick cortices and low minimum breadth, also possessed a

long head-neck axis. Only three complete head neck axes possibly attributable to "erectus" are known. The axial length of Trinil, Femora I and II are both above the Ancaster control means but within that range; KNM ER 999, however, has the longest axial length in the entire series and is more than 2 s.d. units above the Ancaster male mean. Nevertheless, the Neck-Shaft Index shows that the three "erectus" specimens are closely equivalent to the control means. But, using Lovejoy and Heiple's (1970) trigonometrically estimated femoral length for *A. africanus*, this Index is outside the control range, in the case of SK 82 and SK 97.

The morphological complex which characterizes the "australopithecine" femur has been described with reference to the various specimens presently attributed to this group. From the radiological and anatomical evidence of these specimens it can be suggested that the pelvic stabilizing mechanisms operated in a manner different from that found in modern man. The lack of strong vertical cancellous orientation in the greater trochanter of SK 82, SK 97 and OH 20 suggests that the tensile stresses on this structure were not of the same magnitude nor direction as in the controls; the lack of lateral expansion of the trochanter also supports this conclusion. Since the internal and external

structures of the greater trochanter resemble the condition in the pongids a reasonable assumption is that it was subjected to similar biomechanical stresses in both groups. It is therefore possible that gluteus medius and minimus were primarily acting as extensors and not as abductors as they do in modern man. A similar suggestion has been made by Napier (1967). The lateral expansion of the greater trochanter, as seen in the "hominines" would have the biomechanical effect of increasing the abduction moment of gluteus medius and minimus. If, however, bipedality was as well developed in these hominids as seems evident from the specimens then some form of pelvic stabilization on the unsupported side would have been necessary. It is possible that the widely flaring iliac crests present on the known "australopithecine" pelves from South Africa could have provided mechanical advantage for certain abdominal muscles (such as the internal and external obliques) to effect at least partial pelvic stabilization from above.

The probably posterior position of Poirier's facet on SK 82, SK 97 and KNM ER 738 is difficult to fully assess without more complete pelvic material. It may well be due to the combined effects of the flared ilia and more laterally directed acetabula.

Two femoral shafts have been attributed to the "australopithecine" group: KNM ER 736 and 993. As was pointed out in the previous section these two specimens show considerable dissimilarity. Both are robust at the sub-trochanteric level, and in this agree with SK 82 SK 97 and KNM ER 738, but below this level the similarities end. KNM ER 736 continues to be very robust, exceeding both the Ancaster males and the "erectus" means in most parameters; KNM ER 993, however, becomes very gracile in its internal dimensions. This very basic difference, along with those described in the previous section, suggests that both specimens do not belong to the same functional or taxonomic group. KNM ER 736, although possessing parameters above the "erectus" means in most instances, appears to demonstrate a morphological pattern more in agreement with that group than with KNM ER 993 and it is therefore suggested that KNM ER 736 should be attributed to the "erectus" group. The results of the multivariate analyses support this association. The pattern of KNM ER 993, with its comparatively lightly built and curved lower shaft does not resemble any other specimen in this series and because no other complete shafts from the "australopithecines" are known it perhaps should remain with group for the present.

It is apparent, then, that the hominid femoral shaft has undergone a certain amount of remodeling through the Pleistocene. A major indication of this remodeling is found in the Minimum Breadth Index (see Table X). This index suggests that the point of minimum transverse breadth occurred lower on the shaft of the "erectus" group than in the later control population. This finding is further substantiated by the slightly narrower diameters at the sub-pilastric level in the "erectus" shaft.

A further indication of this remodeling can be found at the mid-shaft level. In the controls, the lateral cortex at this level is thicker than the medial; in the fossil sample, with two exceptions - KNM ER 803 and Trinil, Femur I - the medial cortex is thicker than the lateral. A similar relationship is found in the pongids. This suggests that weight was being transferred to the lateral aspect of the shaft at a lower position in the earlier hominids. The explanation of this difference is more likely to be found in evolutionary changes in the pelvis than wholly within the femur, but could, in part, be due to the hypothesized longer head-neck axis in the "erectus" group.

Neandertal, Trinil and to a lesser extent Oberkassel

and Rhodesian, seem to occupy a somewhat intermediate position biometrically between the earlier "erectus" populations and the later controls. This intermediate position has been suggested in the multivariate analyses (see Diagrams II and IV). Especially interesting is the demonstration that at the mid-shaft level the medial cortex in Neandertal is thicker than the lateral - a condition like that found in the earlier specimens. Although the four Trinil femora show considerable variability within themselves they, in general, conform with this pattern and have also been placed in a somewhat intermediate position on Diagrams II and IV. Thus the particular morphological pattern shown by the Trinil specimens does not firmly indicate their association with the "erectus" pattern now emerging from the Peking and East African material; neither does it firmly ally them with the later control group. Neandertal, Oberkassel and Rhodesian all date to the early or middle Wurm and are generally contemporary. There is some uncertainity regarding the date of the Trinil specimens but their morphology more closely allies them with this Wurm group than with either the earlier or later hominines.

V.2: TAXONOMY OF THE FOSSIL HOMINIDAE: A discussion of nomenclature should properly begin with a definition of terms since the words "systematics", "taxonomy" and "classification" have often, incorrectly, been used synonymously. "Systematics" has been defined as "the scientific study of the kinds and diversity of organisms and of any and all relationships among them." "Classification is the ordering of organisms into groups on the basis of their relationships, that is, of associations by contiguity, similarity, or both." "Taxonomy is the theoretical study of classification, including its bases, principles, procedures and rules". (Simpson, 1961).

Taxonomic theory of the modern era, as opposed to that of the Aristotelian and Platonic schools, began with Ray in 1686 (cited by Mayr, 1963). While rejecting the possibility of spontaneous generation of new life Ray attempted to reconcile classical typological classifications, in the Platonic sense, with the observed variation in nature. More importantly, however, Ray set a definition of the morphospecies which has held until well into the present century. Indeed, Ray's concept of the morphospecies (the degree of morphologic similarity can be related to classificatory boundaries) has found new life in the

work of the numerical taxonomists. In addition to this, Ray's work contained the nucleus of perhaps the most widely used of the current neontological species definitions: a biological species based on reproductive isolation.

While Ray contributed to the development of the concept of the species it was Tournefort, who, in 1700 stabilized the concept of the genus (cited by Raven, Berlin and Breedlove, 1971). The groundwork was therefore laid for Linnaeus' contribution of the binomial system in 1735. Linnaean classification is based on the recognition of morphologically or reproductively discontinuous groups; the immutability and fixity of these groups is perhaps the major feature of this system. Indeed, this approach was entirely appropriate in early 18th century Europe when neither evolution nor the perspective of geological time were known. Oddly, it was the development of the science of geology, beginning in that century, which contributed perhaps most heavily to the firm acceptance and establishment of Linnaean taxonomy. With the recognition of geological processes and the stratigraphical progression of rock layers it became necessary to characterize and categorize the newly recovered fossils from those layers. Since the

specimens were isolated, physically, from other related specimens, they formed discontinuous groups. This discontinuity, fortuitous and artificial, qualified them for distinct Linnaean binomials. Thus segments of continuous biological lineages were arbitrarily divided into discontinuous and discrete groups - a system still in almost universal practice today. Only the recovery of "intermediates" could suggest the inappropriateness of the system for the classification of fossil specimens. Thus the Linnaean system has been continued by geologists, stratigraphers and palaeontologists into the present day as a semantic convenience which emphasizes discontinuity while our knowledge of evolutionary process demands the emphasis be placed on continuity.

Mayr, among others, recognized the difficulty in defining and separating fossil species; he stated: "it cannot be denied that an objective delimitation of species in a multidimensional system is an impossibility" (1963). This statement recognizes the impossibility, indeed the invalidity, of drawing finite taxonomic lines between ancestor-descendant populations. The clinal gradients between time successive populations must be as gradual as those between human races today; a higher level of organization will not be reached within the space of a single generation as suggested by those who

draw lines between palaeospecies. The evolution from one species to another involves a number of finite molecular and behavioural steps, each building on the ones before.

Currently, theoretical and practical approaches to the taxonomy of non-living populations centre on the morpho-species concept; this has been defined as "a group of individuals or populations with the same or similar morphological characters" (Mayr, 1942). It must be recognized that all biospecies are also morphospecies but all morphospecies are not demonstrably biospecies. The concept and recognition of the morphospecies in non-living populations faces three important complications; character displacement, phenotypic plasticity and mosaicism in evolution.

The term "character displacement" was first proposed by Brown and Wilson (1959) to describe situations where differences between related populations or species are greater in areas of sympatry than in areas of allopatry. In other words, in areas where related species are in competition for some resources they will show greater morphological divergence from each other than in areas where they are not in competition. Brown (1958) and Schaeffer (1968) have suggested that

character displacement may have been a factor in human evolution. Working on the assumption that two types of hominids existed in the early Pleistocene, Schaeffer demonstrated that the dental apparatus showed greater metric differences in areas where the two types co-occurred. His results suggested that the two hominid populations in Bed I, Olduvai and at Swartkrans showed more divergence from each other than at areas in South Africa (Sterkfontein, Makapansgat and Taung) where only a single type hominid has been found. Results of Schaeffer's comparison of robust to gracile forms in terms of tooth size approached those of Hutchinson (1959) who found that in areas of sympatry a comparison of congeneric populations of some birds and mammals yielded a size ratio of 1:1.28; comparison of allopatric populations yielded a ratio of near unity. There are some difficulties in the validification of Schaeffer's data; primarily, contemporaneity must be demonstrated before populations can be considered sympatric and this is not possible at Swartkrans. It is, however, an interesting and plausible theory and it is a basic tenet of evolutionary theory that competitive pressure will increase variation. It is, moreover, a situation which could distort the parameters of morphospecific criteria and as such must be considered in the definition of palaeospecies.

That phenotypic plasticity is a factor in human diversity was first recognized by Franz Boas (1912). He demonstrated that the American descendants of foreign born immigrants to New York differed metrically, to a significant degree, from their parents. The early studies, based on only a few measurements, demonstrated mainly a decrease in Cephalic Index and an increase in stature among the children of immigrants. Many subsequent and more elaborate studies have demonstrated similar changes. Boas (1912) and Dornfeldt (1941) with Eastern European immigrants to New York, Guthe (1918) with Russian Jews in Boston, Spier (1929) and Ito (1936, 1942) with American born Japanese and Goldstein (1943) with the children of Mexican immigrants to Texas have all reached similar conclusions regarding changes in the F_1 and subsequent generations of immigrant families. A very elaborate study was conducted by Shapiro (1939) into the anthropometry of Hawaiian born children of Japanese immigrants. He found significant increases in the length of most long bones but decreases in the chest diameters, nose breadth and head length. Findings by Lasker (1946) on American born Chinese demonstrated non-metric alterations as well as metric changes. Lasker showed changes in pigmentation of the sclera, frequency of the torus palatinus and pelage density in the immigrants.

The consistent finding of all of these reports is that the F_1 and subsequent generations born in the new environment differ significantly from their ancestral populations. Such changes obviously do not stem from alterations of the genetic material; a more likely explanation involves the recognition that genotypes have variable manifestations and the ultimate phenotype may demonstrate influences of external factors as well as internal factors. Nutrition certainly can be implicated here involving levels of micronutrients (Odum, 1959) as well as the larger dietary components. However, the real etiology of these changes has not been discovered but it probably involves complex interactions between nutritional factors, climate and altitude, at least.

Since virtually all taxonomic levels of fossil hominids are based on morphological criteria the demonstration of phenotypic plasticity in some modern populations is obviously relevant. It is equally obvious that the existence or measurement of plasticity in fossil populations is not demonstrable; nevertheless, its occurrence in modern groups suggests the need for caution in making taxonomic diagnoses, especially at the sub-generic level, based on morphologic criteria alone.

Any classification of fossil hominids, whether it rests

on morphological or biological definitions of the species must consider a further problem. This is perhaps one of the most crucial problems in hominid palaeotaxonomy today and it concerns the theoretical and practical difficulties of reconciling the concept of mosaic evolution with those of Adansonian systematics[1]. These embody paradoxical and irreconcilable views of the dynamics of evolution; each with a profound effect on the practical application of taxonomic theory.

Mosaic evolution is a theoretically attractive concept in many ways but it must be recognized that the fossil evidence for differential evolutionary rates in various anatomical systems within the Hominidae is not unequivocal. The early descriptions of mosaic evolution with regard to hominid evolution (Mayr, 1950; Le Gros Clark, 1950) stressed the discrepancy between cranial capacity and development and pelvic and lower limb development in the South African "australopithecines". It has also been invoked to explain similar suggested differences in the Javan and Chinese fossil hominids of a later date (Le Gros Clark, 1967 and elsewhere). It is suggested here that, with regard to the latter example, the

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1. Adanson, an 18th century botanist, stipulated that in formulating natural or "general" classifications all features must have equal weighting and that the taxonomic criteria reflect correlations between features.

femur at least shows a morphological pattern different from that of a sapient control population and because of this may be an invalid application of the term "mosaic evolution".

Its application to the "australopithecines" may be criticized on two lines. First, although the known femora and pelves of these early hominids show clear adaptations to some form of upright bipedalism they are in no sense "sapient". Nor are they satisfactorily intermediate between the sapient condition and a hypothetical anthropoid ancestor. The wide flare of the "australopithecine" ilium, for example, shows a unique and, as yet, incompletely explained specialization.

Of more basic concern is the difficulty of reconciling mosaic evolution with the theoretical constructs of "synthetic" evolution, as defined by Huxley. While recognizing, on the one hand, that gene pool responses occur in relation to both internal and external stimuli the theory of mosaic development seems to deny the inter relatedness of all such stimuli which are of sufficient force and importance to elicit those responses. The "Washburnian" syndrome (canine reduction, manual prehensility, bipedalism and tool use) while open to question on several points, is a clear theoretical statement of the cohesiveness of effective evolutionary stimuli

and demonstrates the difficulties of visualizing isolated adaptive responses. Ill-adapted or incompletely adapted organisms will not survive in nature; the pressures from a changing environment demand a rapid and relatively complete accommodation and the pressures on the gene pool will be such that a total response must be made rapidly or extinction will ensue.

The postulates of Adansonian systematics demand that one view the specimen and the population as a cohesive, integrated whole. Sneath and Sokal (1962) have recently redefined the aims and potentials of Adansonian systematics in terms of both modern genetic theory and numerical taxonomy. While not actually broadening the original postulates, Sokal and Sneath have rather placed them on a firmer theoretical base with knowledge gained from the field of genetics. Specifically, they have suggested that the equal weighting of characters is validified by the pleiotropic effect of the genes. They suggested that "every taxonomic character is likely to be affected by more than one genetic factor and that conversely most genes affect more than one character, resulting in a complicated nexus of cause and effect ... there are no large and distinct classes of genes affecting exclusively one class of characters (such as morphological, physiological or ethological) or restricted portions of

the organism (such as the head, skeleton, etc.)". (1962). The pleiotropic effect of discrete codons is a well demonstrated and widely accepted feature of current genetic studies.

While Sneath and Sokal did not critically direct their statement toward the theory of mosaic evolution their implications clearly cast doubt on the basic assumptions of that view. It is possible that Mayr and Le Gros Clark in their discussions of differential evolution held perhaps a too simplistic and restricted view of genetic activity under adaptive pressures. It is possible that mosaic evolution, as generally applied to hominid evolution, is, to a degree, incompatible with current views of genetic processes and activities and with the fossil evidence.

The implications of these two opposing views for the application of systematics theory to fossil material is of extreme importance. Implicit in the concept of mosaicism in evolution is the warning that fragmentary fossil material cannot be confidently classified. An isolated limb bone evolving at (say) a faster rate would be placed in a higher evolutionary grade while a skull, more conservative in its evolution, would be placed lower in the schema. This is clearly an unsatisfactory situation.

The question obviously cannot be resolved from a study on a single bone. Multivariate statistics, including Mahalanobis"s D^2, are of some use in suggesting patterns of metric differences but biometric variances between specimens and groups, perhaps widely separated in time, cannot be related to the lower levels of classificatory categories.

Moreover, I have attempted to show in the preceeding pages the difficulties of defining specifically isolated populations in fossil hominid groups. Not only is the application of the species concept to fossil material a contradiction to evolutionary theory the numerous ways in which the phenotype can be altered diminish the possibility that palaeospecies can be recognized and delimited. It is not suggested that fossil hominid species did not objectively exist: it is denied that they can be accurately recognized in the present fossil record.

Traditional taxonomy has attempted to name, to suggest distinctiveness and similarity and to demonstrate phylogeny. This is perhaps too large a task and an impossible one in view of the fragmented nature of the fossil remains. It is suggested here that the most valid, objective and indeed useful, task of hominid

classification is to define lineal arrangements of ancestor-descendant populations. The lineage should not, however, be viewed as a single, unbranching line; it should be viewed as a "plexus" as defined by Trueman (1924). In his terms, a lineal plexus is a "bundle of lines ... which repeatedly branch and re-unite" the individual lines representing sub-specific categories. It is suggested that the lineal plexus, with reference to hominid evolution, can most conveniently and objectively be defined through the application of generic criteria. The genus does not rest on morphological criteria alone, but, as defined by Mayr (1950) rests also with the implication of the morphology for adaptive behaviour. Thus the "adaptive plateau" occupied by a single genus represents a larger ecological zone and behavioural territory than the niche occupied by the species.

The femora included in this study fell into two morphological patterns; as suggested by the multivariate statistics, they were separated by a wide biometric gap. The two groups locally co-existed, probably for a considerable period and, unavoidably, would have been in competition for some resources. Nevertheless, the ecological zone occupied by each was different enough to permit the continuation of sympatry. This evidence is interpreted to mean that the groups

were separate at the generic level; division of the respective genera into smaller classificatory categories would be impossible to validify on the basis of the presently available evidence. Nevertheless, the "erectus" group presents a morphological pattern distinct from that of the Ancaster control group. It is therefore suggested that this group be considered as a grade within the genus *Homo*.

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TABLE IX

EXTERNAL SHAFT INDICES

	PLATYMERIC INDEX				PILASTRIC INDEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	78.75	8.29	1.09	64.4-108.5	102.52	7.17	0.95	88.90-123.50
Females = 43	78.77	8.80	1.34	62.6-107.3	98.19	16.01	2.44	90.90-117.50
Bushmen = 8	83.11	7.29		71.7± 94.3	111.96	11.67		99.5 -135.5
Pan = 3	84.66	3.41		81.5-103.7	92.70	9.88		83.3 - 97.8
Gorilla = 3	91.93	10.35		85.2-104.1	91.80	6.79		78.3 - 99.2
Pongo = 3	70.60	2.19		68.4- 73.6	76.07	2.35		72.1 - 80.3
Spy 8	71.5				99.5			
16	73.9				100.5			
Neandertal R.	84.5				109.0			
L.	70.0				106.0			
Oberkassel L. Male	82.8				111.3			
R. Female	74.0				108.0			
Rhodesian 689	83.0							
907	85.5				102.1			
690	67.7							
Peking, Femur I	67.8				89.3			
Femur IV	77.0				83.1			
Trinil, Femur I	89.1				107.1			
Femur II	79.7				96.3			
Femur III	76.1				100.7			
Femur IV	73.6				90.2			
OH 28	62.0				79.5			

TABLE IX
(continued)

	PLATYMERIC INDEX	PILASTRIC INDEX
KNM ER 736	80.1	99.2
737	98.9	81.9
738	81.2	
803	77.0	90.0
815	70.5	
993	78.6	96.8
999	87.1	111.4
SK 82	82.9	
SK 97	80.1	

TABLE X

EXTERNAL SHAFT INDICES

	MINIMUM BREADTH INDEX				SUB-PILASTRIC INDEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 53	54.67	7.60	1.00	42.9-74.0	106.65	10.69	1.41	80.6-143.2
Females = 47	56.10	7.41	1.13	44.3-70.7	111.96	7.16	1.09	95.3-131.8
Bushmen = 8	59.81	6.72		50.1-75.9	99.46	2.82		85.2-114.2
Pan = 3	71.6	9.69		58.3-79.2	115.16	3.69		106.4-132.4
Gorilla = 3	73.7	0.68		73.1-74.7	134.70	8.09		107.3-152.9
Pongo = 3	73.9	5.51		66.1-77.9	131.76	5.48		125.6-138.9
Spy 8	61.0				96.5			
Neandertal R.	48.2				100.8			
L.	51.0				95.2			
Oberkassel R. female	-				85.9			
L. male	55.7				104.3			
Peking, Femur IV	45.5				111.2			
Trinil, Femur I	47.3				122.0			
Femur II	56.3				99.6			
Femur III	47.5				101.1			
Femur IV	50.7				102.6			
OH 28	-				120.5*			
KNM ER 737	45.4				108.0*			
993	51.3				99.3			
999	48.5							
803	-				99.3*			
736	-				110.4			

* Taken at most distal point remaining on shaft.

TABLE XI

POPLITEAL INDEX

	mean	s.d.	standard error of m	range
Ancaster				
Males = 57	74.14	5.34	0.70	63.9-87.0
Females = 43	72.36	7.27	1.10	62.3-98.7
Bushmen = 8	71.40	8.20		55.1-81.4
Pan = 3	62.16	1.86		58.9-65.1
Gorilla = 3	55.10	4.59		48.9-60.0
Pongo = 3	54.80	0.84		54.5-56.3

Spy 8		73.4
Neandertal	R.	75.5
	L.	64.0
Oberkassel	L. Male	62.1
	R. Female	46.0
Rhodesian 689		76.0
Peking, Femur IV		96.1
Trinil, Femur I		88.9
Femur II		108.1
Femur III		78.1
Femur IV		96.2
Omo		71.6
KNM ER 993		71.1*
TM 1513		63.5*
STS 34		71.4*

* Measurements taken at 2 cm. above the anterior superior articular margin

All measurements in mm.

TABLE XII

	HEAD DIAMETER				LENGTH OF HEAD-NECK AXIS			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males N=57	48.94		0.37	42.1-53.0	78.28	6.02	0.79	65.9-90.9
Females N=43	43.02	2.44	0.37	39.2-49.1	68.19	5.72	0.87	60.0-86.3
Bushmen N= 8	38.01	2.39		35.0-41.8	59.56	3.79		54.0-65.9
Pan N= 3	34.73	1.36		32.2-36.0	59.30	5.61		55.2-67.5
Gorilla N= 3	37.01	0.70		36.0-37.5	66.00	1.08		66.0-68.9
Pongo N= 3	38.76	1.19		37.2-40.1	62.30	4.65		56.0-66.0

Spy	54.8	-
Neandertal R.	56.2	82.9
Oberkassel L. Male	51.9	77.3
Trinil, Femur I	41.0	83.1
Femur II	-	82.0 (est.)
Rhodesian 689	49.5	88.0
907	55.0	89.1
KNM ER 738	34.9	59.0
999	51.1	98.1
SK 82	33.8	69.9
SK 97	37.2	68.8

all measurements in mm.

TABLE XIII

	HEAD/NECK INDEX				NECK/SHAFT INDEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	62.80	5.19	0.68	51.3-74.5	20.51	1.73	0.23	16.6-25.7
Females = 43	63.33	4.40	0.67	53.4-71.7	19.72	1.52	0.23	16.7-23.3
Bushmen = 8	64.1	3.98		60.6-68.7	17.12	1.10		15.8-18.2
Pan = 3	58.6	4.92		53.3-65.2	2211	1.28		20.9-23.9
Gorilla = 3	56.6	1.08		54.5-56.8	23.2	2.28		21.6-26.5
Pongo = 3	62.4	3.01		61.8-66.4	26.9	0.51		25.9-27.6
Neandertal R.	67.8				21.8			
Oberkassel L. Male	67.1				20.4			
Trinil, Femur I	58.7				17.3			
Rhodesian 689	60.0							
907	63.0							
KNM ER 738	59.0							
999	52.4				20.8			
SK 82	48.0							
SK 97	54.0							

TABLE XIV

SHAFT BOWING: HEIGHT OF SUBTENSE

	mean	s.d.	standard error of m	range
Ancaster				
Males = 57	5.92	2.24	0.29	1.2- 8.6
Females = 43	4.50	1.79	0.27	1.8-13.8
Bushmen = 8	8.64	8.30		5.5-10.8
Pan = 3	7.03	2.50		6.3- 8.9
Gorilla = 3	5.17	2.59		4.8- 5.9
Pongo = 3	3.31	1.75		3.4- 4.2

Neandertal R.	12.40
Oberkassel L. Male	6.60
Peking, Femur IV	4.50
Trinil, Femur I	5.40
Femur II	4.41
KNM ER 737	5.02
993	10.11

All measurements in mm.

TABLE XV

INTERNAL SHAFT DATA

SUB-TROCHANTERIC LEVEL

	MEDIAL CORTEX				LATERAL CORTEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	8.53	2.23	0.29	4.2-17.4	7.21	1.40	0.18	5.0-10.2
Females = 43	6.62	1.35	0.20	4.2-10.0	6.28	1.20	0.18	4.2- 9.6
Bushmen = 8	6.28	1.02		4.1- 7.0	6.71	1.56		4.2- 9.0
Pan = 3	5.96	0.80		5.2- 6.8	5.63	0.89		4.6- 6.2
Gorilla = 3	5.46	1.32		4.3- 6.9	6.13	2.05		4.8- 8.5
Pongo = 3	6.10	0.17		5.9- 6.2	5.16	1.84		4.1- 7.3
Neandertal R.	10.2				9.8			
L.	10.4				12.0			
Oberkassel L. Male	7.0				6.6			
Rhodesian 689	9.0				5.0			
907	8.9				5.0			
Peking, Femur I	10.3				7.8			
Femur IV	8.8				8.8			
Trinil, Femur I	8.0				12.0			
Femur II	6.6				6.8			
Femur III	10.1				7.6			
Femur IV	8.8				7.4			
OH 28	9.0				9.6			
KNM ER 736	9.5				9.0			
737	11.5				9.8			
738	6.9				6.1			
803	7.5				6.1			
993	10.4				8.1			
999	8.3				6.6			
SK 82	9.1				9.9			
SK 97	8.1				6.0			

All measurements in mm.

TABLE XVI

INTERNAL SHAFT DATA

SUB-TROCHANTERIC LEVEL

	POSTERIOR CORTEX				ANTERIOR CORTEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	5.69	1.42	0.18	2.8-9.6	5.10	1.06	0.14	3.6-10.6
Females = 43	4.76	1.47	0.22	2.6-9.8	4.37	0.83	0.12	3.0- 6.6
Bushmen = 8	5.02	0.83		3.9-5.9	4.91	1.12		3.1- 6.0
Pan = 3	5.56	0.65		4.9-6.2	4.90	0.17		4.8- 5.1
Gorilla = 3	5.26	2.37		3.3-7.2	4.90	2.02		3.4- 7.2
Pongo = 3	5.16	1.19		3.8-6.0	4.96	0.85		4.1- 5.8
Neandertal R	7.2				7.6			
L	8.0				7.4			
Oberkassel L. Male	5.4				5.2			
Rhodesian 689	6.1				6.0			
907	8.1				5.1			
Peking, Femur I	8.6				6.2			
Femur IV	8.1				6.1			
Trinil, Femur I	10.0				8.6			
Femur II	7.1				5.4			
Femur III	8.2				5.0			
Femur IV	5.2				4.2			
OH 28	5.8				4.6			
KNM ER 736	6.8				5.4			
737	5.8				6.8			
738	5.8				5.8			
803	6.1				6.1			
993	9.8				8.7			
999	5.5				3.7			
SK 82	8.3				6.5			
SK 97	6.2				6.3			

All measurements in mm.

TABLE XVII

INTERNAL SHAFT DATA

MID-SHAFT LEVEL

	MEDIAL CORTEX				LATERAL CORTEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	7.95	1.42	0.18	4.6-12.8	8.27	1.16	0.15	4.0-10.4
Females = 43	7.11	1.11	0.17	4.6-10.0	7.03	1.53	0.23	4.0-13.2
Bushmen = 8	5.68	0.57		4.6- 6.2	6.51	0.82		5.3- 7.2
Pan = 3	6.16	0.65		5.5- 6.8	4.76	0.40		4.3- 5.0
Gorilla = 3	6.13	1.37		4.1- 6.5	5.20	1.21		5.1- 7.7
Pongo = 3	6.26	0.40		5.9- 6.7	5.90	0.52		5.3- 6.3
Neandertal R	8.0				6.4			
L	8.6				7.6			
Oberkasses L Male	7.0				7.0			
Rhodesian 689	7.2				7.5			
Peking, Femur I	11.5				9.5			
Femur IV	10.3				9.5			
Trinil, Femur I	8.0				9.0			
Femur II	7.8				6.6			
Femur III	8.0				7.8			
Femur IV	8.6				6.6			
OH 28	9.2				7.6			
KNM ER 736	9.3				8.6			
737	10.5				8.9			
803	6.2				7.2			
993	6.8				6.4			
999	7.3				5.6			

All measurements in mm.

TABLE XVIII

INTERNAL SHAFT DATA

MID-SHAFT LEVEL

	POSTERIOR CORTEX				ANTERIOR CORTEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	9.71	1.83	0.24	5.2-16.0	5.62	1.02	0.13	2.2-7.6
Females = 43	7.80	1.30	0.19	5.4-10.8	4.87	1.26	0.19	1.4-9.8
Bushmen = 8	8.38	1.03		6.8-9.6	5.16	1.29		4.0-6.1
Pan = 3	4.70	0.34		4.5- 5.1	4.26	0.35		3.9-4.6
Gorilla = 3	5.76	1.85		4.1- 7.9	5.30	1.51		4.1-7.0
Pongo = 3	5.33	1.00		4.2- 5.7	4.86	0.90		4.0-5.8
Neandertal R	8.8				6.2			
L	10.4				6.6			
Oberkassel L Male	8.6				4.6			
Rhodesian 689	6.8				7.5			
Peking, Femur I	9.0				7.9			
Femur IV	9.6				6.5			
Trinil, Femur I	10.1				5.2			
Femur II	7.8				4.8			
Femur III	10.4				5.6			
Femur IV	8.4				7.8			
OH 28	6.2				5.2			
KNM ER 736	10.8				7.2			
737	6.6				11.5			
803	7.1				5.4			
993	4.8				3.9			
999	9.2				5.7			

All measurements in mm.

TABLE XIX

INTERNAL SHAFT DATA

SUB-PILASTRIC LEVEL

	MEDIAL CORTEX				LATERAL CORTEX			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	4.44	1.03	0.13	2.0-7.0	4.45	0.88	0.11	2.4-6.0
Females = 43	4.11	0.87	0.13	2.6-7.2	3.60	0.86	0.13	1.6-6.0
Bushmen = 8	3.92	0.57		3.7-4.9	3.73	0.60		3.3-4.7
Pan = 3	4.50	0.96		3.8-5.6	4.30	0.72		3.9-5.1
Gorilla = 3	3.70	1.30		2.4-5.0	3.53	0.40		3.1-3.9
Pongo = 3	4.20	0.36		3.9-4.6	3.66	0.49		3.1-4.0

Neandertal	R.	4.4	2.8
	L.	3.4	3.6
Oberkassel	L. Male	3.8	4.6
Rhodesian	689	4.4	5.1
Trinil,	Femur I	5.2	5.8
	Femur II	7.0	6.6
	Femur III	6.I	7.0
	Femur IV	6.2	5.6
OH 28		4.6	5.4
KNM ER	736	4.7	6.1
	737	6.2	7.2
	993	2.9	3.9

All measurements in mm.

TABLE XX

INTERNAL SHAFT DATA

SUB-PILASTRIC LEVEL

	POSTERIOR CORTEX				ANTERIOR CORTEX			
	mean	s.d.	standard error of $\bar{m}$	range	mean	s.d.	standard error of $\bar{m}$	range
Ancaster								
Males = 57	5.22	1.49	0.19	3.0-12.0	4.41	1.04	0.13	1.4-6.6
Females = 43	4.98	1.95	0.29	3.0-11.4	3.70	0.90	0.13	1.1-5.0
Bushmen = 8	5.48	1.50		4.1- 8.5	3.72	0.69		3.2-5.5
Pan = 3	4.46	0.98		3.9- 5.6	4.16	0.63		3.8-4.9
Gorilla = 3	4.96	0.86		4.2- 5.9	3.66	0.68		2.9-4.8
Pongo = 3	5.16	0.64		4.7- 5.9	4.03	0.32		3.8-4.4
Neandertal R.	4.8				5.2			
L.	4.0				3.8			
Oberkassel L. Male	5.2				3.4			
Rhodesian 689	7.1				6.1			
Trinil, Femur I	5.8				4.1			
Femur II	9.0				6.3			
Femur III	9.4				4.4			
Femur IV	5.1				4.6			
OH 28	5.4				3.6			
KNM ER 736	8.1				7.6			
737	5.5				7.9			
993	4.1				3.1			

All measurements in mm.

TABLE XXI

CORTICAL INDICES

SUB-TROCHANTERIC LEVEL

	MEDIOLATERAL				ANTEROPOSTERIOR			
	mean	s.d.	standard error of $\bar{m}$	range	mean	s.d.	standard error of $\bar{m}$	range
Ancaster								
Males = 57	46.22	9.30	1.23	29.6-74.6	40.25	7.62	1.01	26.9-62.3
Females = 43	41.60	9.94	1.15	29.6-60.9	37.90	10.46	1.59	26.9-69.7
Bushmen = 8	52.39	7.58		35.9-59.2	48.96	9.97		30.6-61.8
Pan = 3	42.90	5.45		35.3-49.1	45.67	2.68		48.6-52.0
Gorilla = 3	37.43	6.55		32.1-46.7	36.23	12.72		23.8-53.7
Pongo = 3	42.70	6.61		37.2-51.7	54.30	8.60		42.9-62.8
Neandertal R.	59.2				51.9			
L.	58.4				59.2			
Oberkassel L. Male	42.2				44.4			
Rhodesian 689	41.0				43.0			
907	40.5				44.7			
Peking, Femur I	52.9				63.8			
Femur IV	52.5				54.7			
Trinil, Femur I	62.8				63.1			
Femur II	41.9				48.6			
Femur III	53.3				52.6			
Femur IV	48.6				38.4			
OH 28	50.1				45.2			
KNM ER 736	50.1				40.0			
737	59.1				48.5			
738	48.0				47.3			
803	40.1				44.1			
993	56.6				72.0			
999	37.5				24.2			
SK 82	63.5				40.7			
SK 97	46.8				41.8			

TABLE XXII

CORTICAL INDICES

MID-SHAFT

	MEDIOLATERAL				ANTEROPOSTERIOR			
	mean	s.d.	standard error of m	range	mean	s.d.	standard error of m	range
Ancaster								
Males = 57	52.99	7.83	1.03	29.6-74.5	57.65	7.62	1.00	32.8-78.5
Females = 43	49.70	11.16	1.70	27.8-75.8	54.14	11.63	1.72	31.3-71.4
Bushmen = 8	57.10	10.24		43.1-78.3	56.08	5.63		44.2-61.7
Pan = 3	38.60	3.18		35.5-42.2	43.00	2.19		39.9-44.7
Gorilla = 3	40.10	8.15		31.2-50.9	38.13	6.29		33.3-47.0
Pongo = 3	52.50	6.79		42.9-57.5	47.77	4.81		42.3-52.2
Neandertal R.	46.9				52.7			
L.	54.8				54.0			
Oberkassel L. Male	52.4				56.5			
Rhodesian 689	57.0				51.0			
Peking, Femur I	63.3				70.2			
Femur IV	65.7				67.1			
Trinil, Femur I	50.7				61.2			
Femur II	48.1				52.9			
Femur III	58.8				58.5			
Femur IV	62.8				53.1			
OH 28	46.0				53.8			
KNM ER 736	50.1				49.4			
737	66.5				60.4			
803	43.6				42.0			
993	32.0				47.0			
999	39.2				37.8			

TABLE XXIII

CORTICAL ROBUSTICITY

	mean	s.d.	standard error of m	range
Ancaster				
Males = 57	3.96	0.66	0.87	2.60-5.60
Females = 43	3.65	0.76	0.11	2.71-5.00
Bushmen = 8	3.97	0.46		3.60-5.01
Pan = 3	3.36	1.90		3.00-3.70
Gorilla = 3	3.86	0.35		3.20-4.91
Pongo = 3	4.36	0.90		4.00-4.51

Neandertal R.	4.0
L.	4.5
Oberkassel L. Male	3.6
Rhodesian 689	3.7
Peking, Femur I	4.9
Femur IV	4.6
Trinil, Femur I	3.8
Femur II	3.2
Femur III	4.0
Femur IV	4.3
OH 28	2.9
KNM ER 736	4.6
737	4.4
993	3.2
999	3.1

TABLE XXIV

D^2 VALUES

	D^2 from Ancaster	posterior probability	D^2 from "erectus"	posterior probability	D^2 from *Pan*	posterior probability	D^2 from *Gorilla*	posterior probability	D^2 from *Pongo*	posterior probability
Neandertal	52.168	.955	73.670	.045	102.779	.000	132.167	.000	167.735	.000
Trinil, Femur I	83.190	.000	83.745	1.000	141.284	.000	180.007	.000	227.101	.000
Femur II	50.096	1.000	117.627	.000	78.526	.000	138.072	.000	151.940	.000
Femur III	35.567	1.000	86.597	.000	76.089	.000	116.897	.000	132.882	.000
Femur IV	40.818	.905	73.232	.095	78.315	.000	131.408	.000	138.934	.000
Peking, Femur IV	99.838	.977	23.818	.023	164.382	.000	199.459	.000	217.695	.000
OH 28	70.749	.000	26.813	1.000	101.054	.000	159.472	.000	169.027	.000
KNM ER 736	128.249	1.000	129.472	.000	142.497	.000	193.991	.000	203.880	.000
737	86.623	1.000	102.857	.000	106.824	.000	144.814	.000	174.250	.000
993	62.357	.000	112.053	.000	36.574	1.000	65.120	.000	71.572	.000
999	152.890	.000	158.897	1.000	184.801	.000	225.128	.000	270.578	.000
Pan	49.131	.000	143.429	.000	10.530	1.000	39.423	.000	35.551	.000
Gorilla	86.162	.000	208.423	.000	47.103	.000	21.603	1.000	55.410	.000
Pongo	85.627	.000	200.816	.000	34.083	.000	42.992	.000	9.108	1.000

TABLE XXV

COEFFICIENTS OF CORRELATION

ANCASTER

	Head Diameter		Neck Length		Head-Neck Index	
Sub-Trochanteric Level:						
	males	females	males	females	males	females
Medial Cortex	-.0828	.2062	.4218	.5072	-.4798	-.4371
Lateral Cortex	-.0155	.3355	.1599	.3992	-.1752	-.1943
Transverse Shaft	.2708	.4957	.6033	.6133	-.3744	-.3012
Mid-Shaft Level:						
Medial Cortex:	.0324	.3489	.3000	.1606	-.2787	-.2914
Lateral Cortex:	.2894	.0465	.5675	.4331	-.3470	-.4932
Transverse Shaft:	.2594	.5939	.5767	.6701	-.3565	-.2753
Circumference:	.2380	.5800	.1723	.5580	.0177	-.1437
Sub-Pilastric Level:						
Medial Cortex:	-.0888	.1076	-.0183	-.0241	-.0569	.1293
Lateral Cortex:	.0640	.1798	.2826	.3678	-.2266	-.2787
Transverse Shaft:	.2317	.5830	.1911	.6240	-.0098	-.2320
Head Diameter			.3147	.6122		

Males N = 57
Females N = 43

TABLE XXV

(continued)

	anterior cortex mid-shaft		posterior cortex mid-shaft		anterior cortex sub-pilastric		posterior cortex sub-pilastric	
	males	females	males	females	males	females	males	females
length of sub-tense	.2003	.1333	-.0237	-.2593	.3231	.3398	.0738	-.0271

	anterior cortex sub-trochanteric		posterior cortex sub-trochanteric	
length of sub-tense	-.1012	.3231	-.0144	.1007

	transverse diam. mid-shaft		Min. Br. Ix.		Pilastric Ix.		Sub-Pilastric Ix.	
Platymeric Index	-.3041	-.0840	.3251	.3433	.4345	.1153	-.2097	-.1222

	Min. Br. Ix.	
Length of Head-Neck Axis	-.4086	-.0955

TABLE XXVI

GROUP MEANS

	ANCASTER male	s.d.	female	s.d.	combined	s.d.	BUSHMEN group mean	s.d.	"ERECTUS" group mean	s.d.	"A'PITHECUS" group mean	s.d.
sub-trochanteric												
medial cortex	8.53	2.23	6.62	1.35	7.71	2.12	6.28	1.02	8.96[1]	1.39	8.11[2]	1.48
lateral cortex	7.21	1.40	6.28	1.20	6.81	1.39	6.71	1.56	8.27	1.78	7.10	1.85
posterior cortex	5.69	1.42	4.76	1.47	5.29	1.50	5.02	0.83	7.02	1.60	5.91	2.67
Anterior cortex	5.10	1.06	4.37	0.83	4.79	1.03	4.91	1.12	5.60	1.41	6.26	1.09
M-L Cortical Ix.	46.22	9.30	41.60	9.94	44.23	9.80	52.42	7.84	49.88	8.12	53.72	7.84
A-P Cortical Ix.	40.25	7.62	37.90	10.46	39.24	8.98	48.96	10.64	48.32	11.66	43.26	
transverse shaft	34.23	3.10	30.40	2.39	32.58	3.39	24.75	2.17	34.64	2.49	29.95	2.28
A-P shaft	26.99	2.12	23.86	2.23	25.64	2.66	20.47	1.59	26.38	3.55	24.15	1.57
Platymeric Index	78.75	8.29	78.77	8.80	78.76	8.47	83.11	7.95	78.83	10.66	78.90	1.69
mid-shaft												
medial cortex	7.95	1.42	7.11	1.11	7.59	1.36	5.68	0.57	8.74	1.62		
lateral cortex	8.27	1.16	7.03	1.53	7.74	1.46	6.51	0.82	7.83	1.35		
posterior cortex	9.71	1.83	7.80	1.30	8.89	1.87	8.38	1.03	8.37	1.55		
anterior cortex	5.62	1.02	4.87	1.26	5.30	1.18	5.16	1.29	6.56	2.04		
M-L Cortical Ix.	52.99	7.83	49.70	11.18	51.50	9.50	57.18	10.41	54.47	10.08		
A-P Cortical Ix.	57.65	7.62	54.14	11.33	56.14	9.51	56.07	6.08	55.70	10.14		
transverse shaft	28.14	1.51	25.28	1.57	26.91	2.09	21.81	1.04	29.93	2.35		
A-P shaft	28.80	2.13	25.25	1.89	27.28	2.68	24.50	3.73	22.87	3.94		

1. Group composed of Peking, Trinil, OH 28, KNM ER 737, 803 and 999 unless otherwise noted.
2. Group composed of SK 82, 97, KNM ER 738 unless otherwise noted.

TABLE XXVI
(continued)

	ANCASTER male	s.d.	female	s.d.	combined	s.d.	BUSHMEN group mean	s.d.	"ERECTUS" group mean	s.d.
mid-shaft										
Pilastric Ix.	102.52	7.17	98.19	16.01	100.66	11.94	111.96	12.47	93.03	10.87
circumference	88.58	14.50	81.02	4.84	85.33	11.96	75.00	7.43	78.83[1]	10.66
Min. trans. br.	27.39	1.49	24.36	2.58	26.09	2.52	21.38	0.95	25.00[1]	1.84
Cortical Rob. Ix.	3.96	0.66	3.65	0.76	3.83	0.71	3.97	0.50	3.52	1.40
sub-pilastric										
medial cortex	4.44	1.03	4.11	0.87	4.30	0.97	3.92	0.57	4.45	1.04
lateral cortex	4.45	0.88	3.60	0.86	4.08	0.97	3.73	0.60	4.24	1.04
posterior cortex	5.22	1.49	4.98	1.95	5.12	1.70	5.48	1.50	5.11	2.02
transverse shaft	31.36	2.66	28.16	1.87	29.98	2.83	24.52	2.55	28.60	3.44
A-P shaft	29.34	2.67	25.42	2.19	27.65	3.14	24.91	3.64	26.55	3.17
Sub-Pilastric IX	106.65	10.69	111.96	7.16	108.94	9.66	99.46	11.16	107.33	

1. Group composed of Peking, Trinil and OH 28, on this page, unless otherwise noted.

TABLE XXVI

(continued)

	ANCASTER male	s.d.	female	s.d.	combined	s.d.	BUSHMEN group mean	s.d.	"ERECTUS" group mean	s.d.
lower shaft										
transverse shaft	42.81	3.61	37.82	2.60	40.31	3.01	35.95	1.25	39.50[1]	5.07
A-P shaft	31.69	2.65	27.26	3.14	29.47	2.89	25.56	8.89	30.35	4.07
Popliteal Index	74.14	5.34	72.36	7.27	73.21	6.30	62.91	2.17		
sub tense	5.92	2.24	4.50	1.79	5.21	2.01	8.64	2.83	5.70	2.54
chord, total length	287.22	17.71	257.93	15.95	272.52	16.83	260.70	9.07	274.55	
chord, sub length	188.15	26.53	161.88	29.78	175.01	28.15	140.50	4.82	171.99	
shaft length	383.64	20.38	343.97	15.67	363.30	18.02	346.90	12.12		
height of min. br.	208.40	31.25	209.67	10.16	208.96	19.35	207.00	32.54	191.50	18.50
head diameter	48.94	2.83	43.02	2.44	45.98	2.63	38.00	1.32		
head-neck axis	78.28	6.02	68.19	5.72	73.23	5.87	59.34	2.08		
Head-Neck Index	62.80	5.19	63.33	4.40	63.01	4.79	55.09	1.93		
Neck-Shaft Index	20.51	1.73	19.72	1.52	20.01	0.62	15.15	5.21		
Minimum Breadth Ix.	54.67	7.60	56.10	7.41	55.29	7.52	59.81	9.88		

1. Group composed of Peking, Trinil and OH 28

All measurements in mm.

TABLE XXVII

D^2 VALUES

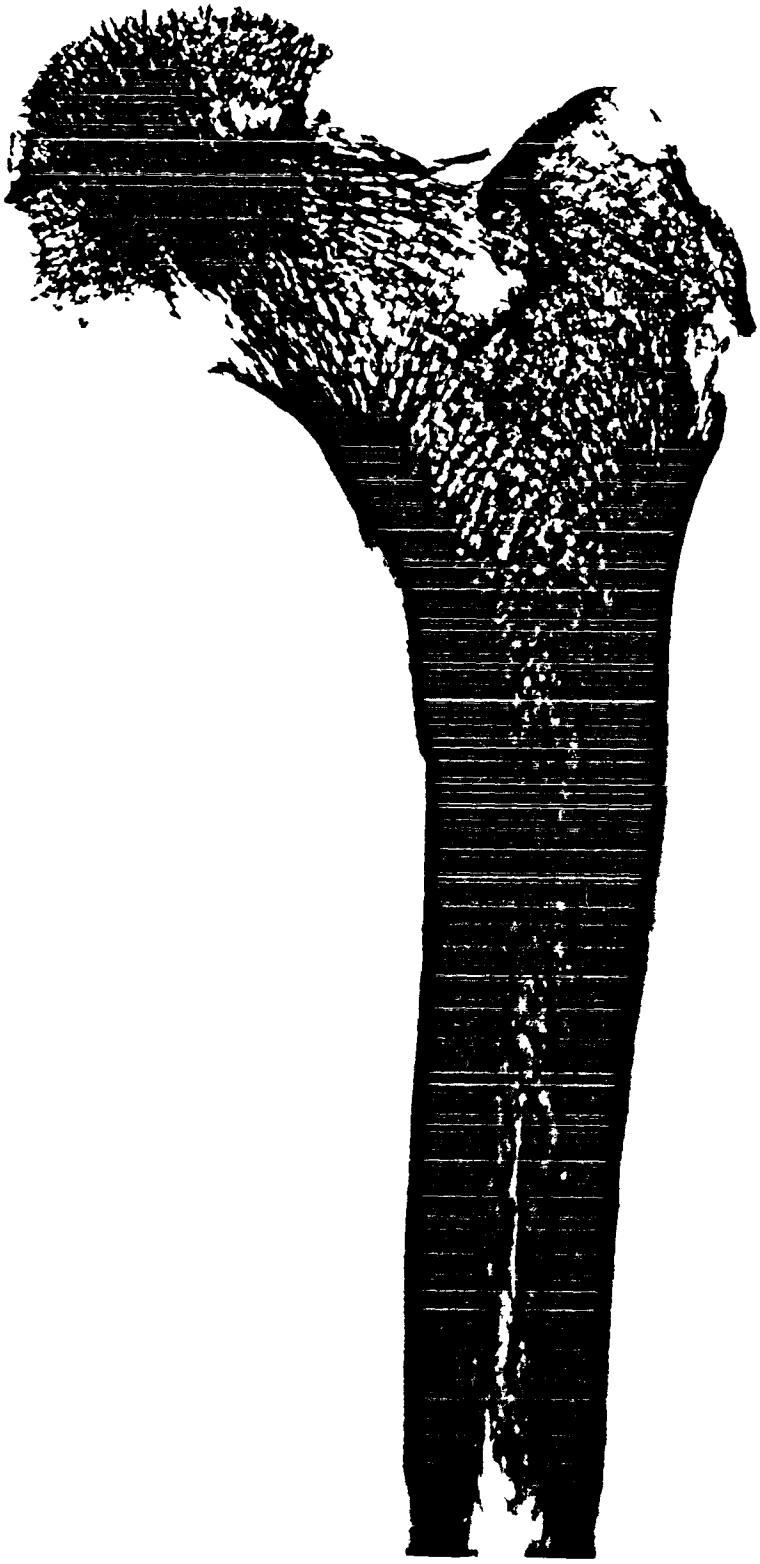
	D^2 from Ancaster	posterior probability	D^2 from "erectus"	posterior probability	D^2 from "australopithecus"	posterior probability
Neandertal	15.868	.283	14.013	.715	135.355	.000
Peking, Femur I	23.322	.010	14.210	.978	150.828	.000
Femur IV	14.891	.049	8.953	.951	148.176	.000
Trinil, Femur I	35.419	.633	36.514	.366	128.660	.000
Femur II	8.555	.145	5.005	.855	131.182	.000
Femur III	8.699	.471	8.467	.529	154.599	.000
Femur IV	18.810	.027	11.614	.973	179.617	.000
OH 28	23.412	.002	10.909	.998	156.336	.000
KNM ER 736	34.175	.045	29.304	.515	174.728	.000
737	67.646	.000	42.938	1.000	197.627	.000
738	276.889	.000	277.169	.000	82.054	1.000
803	87.247	.000	60.974	1.000	255.215	.000
993	60.882	.000	58.907	.000	87.402	.000
999	32.227	.133	28.477	.867	203.964	.000
SK 82	212.308	.000	218.234	.000	41.534	1.000
SK 97	284.289	.000	284.524	.000	38.187	1.000

TABLE XXVII

(continued)

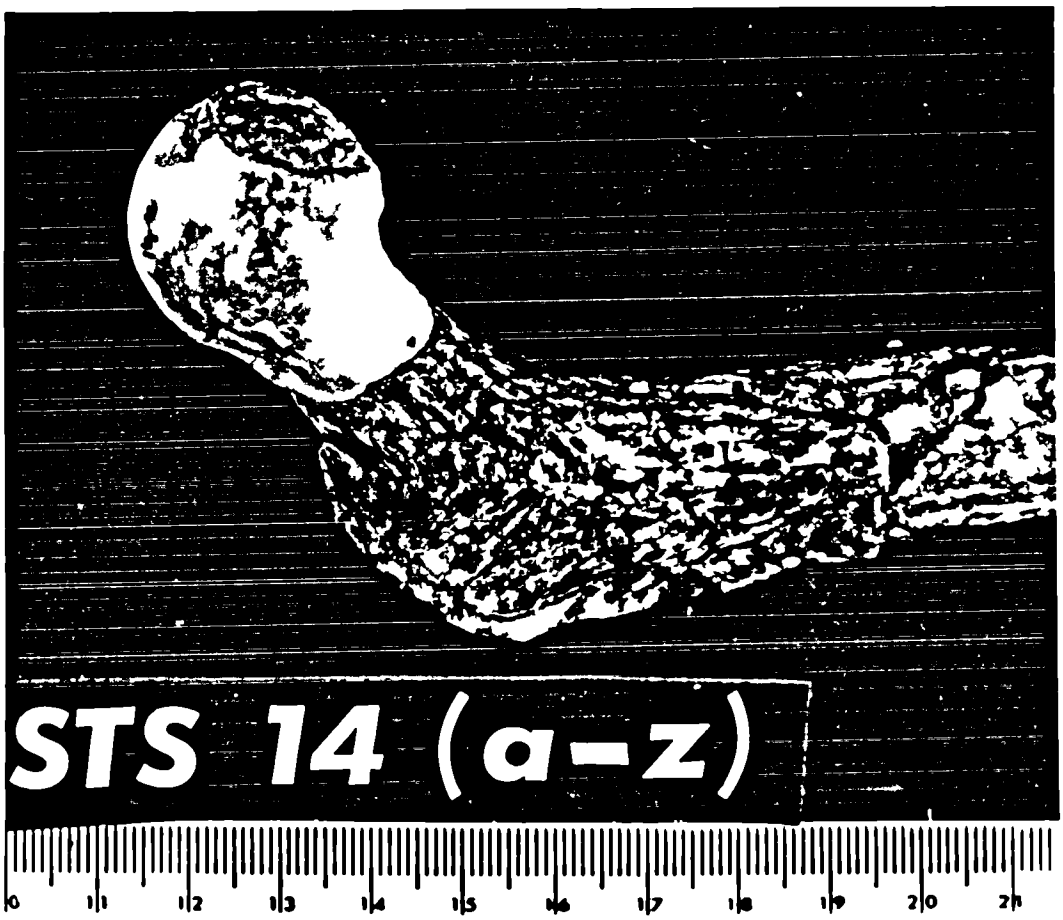
	D^2 from *Pan*	posterior probability	D^2 from *Gorilla*	posterior probability	D^2 from *Pongo*	posterior probability
Neandertal	25.517	.002	54.634	.000	44.675	.000
Peking, Femur I	23.071	.012	45.308	.000	29.880	.000
Femur IV	27.148	.000	43.139	.000	32.572	.000
Trinil, Femur I	48.375	.001	85.899	.000	76.790	.000
Femur II	19.626	.001	38.780	.000	30.191	.000
Femur III	36.436	.000	55.453	.000	47.197	.000
Femur IV	35.452	.000	43.744	.000	41.879	.000
OH 28	31.595	.000	41.091	.000	35.357	.000
KNM ER 736	29.712	.420	35.864	.019	43.769	.000
737	69.464	.000	85.106	.000	81.856	.000
738	246.346	.000	279.986	.000	282.391	.000
803	136.202	.000	147.783	.000	134.745	.000
993	25.864	.995	49.571	.000	36.660	.005
999	54.307	.000	64.573	.000	79.192	.000
SK 82	183.569	.000	222.339	.000	216.187	.000
SK 97	243.387	.000	286.166	.000	274.151	.000

PLATE 1



NEANDERTAL

PLATE II

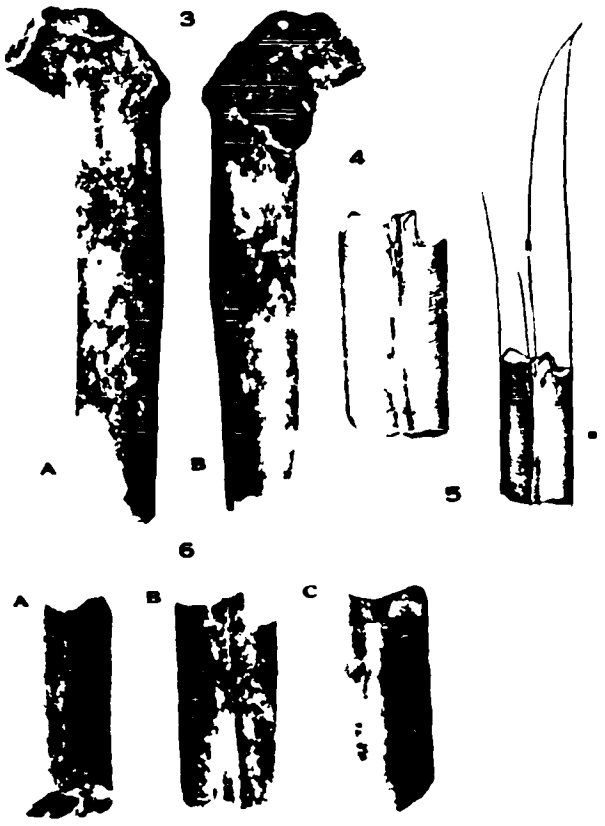


STS 14

PLATE III

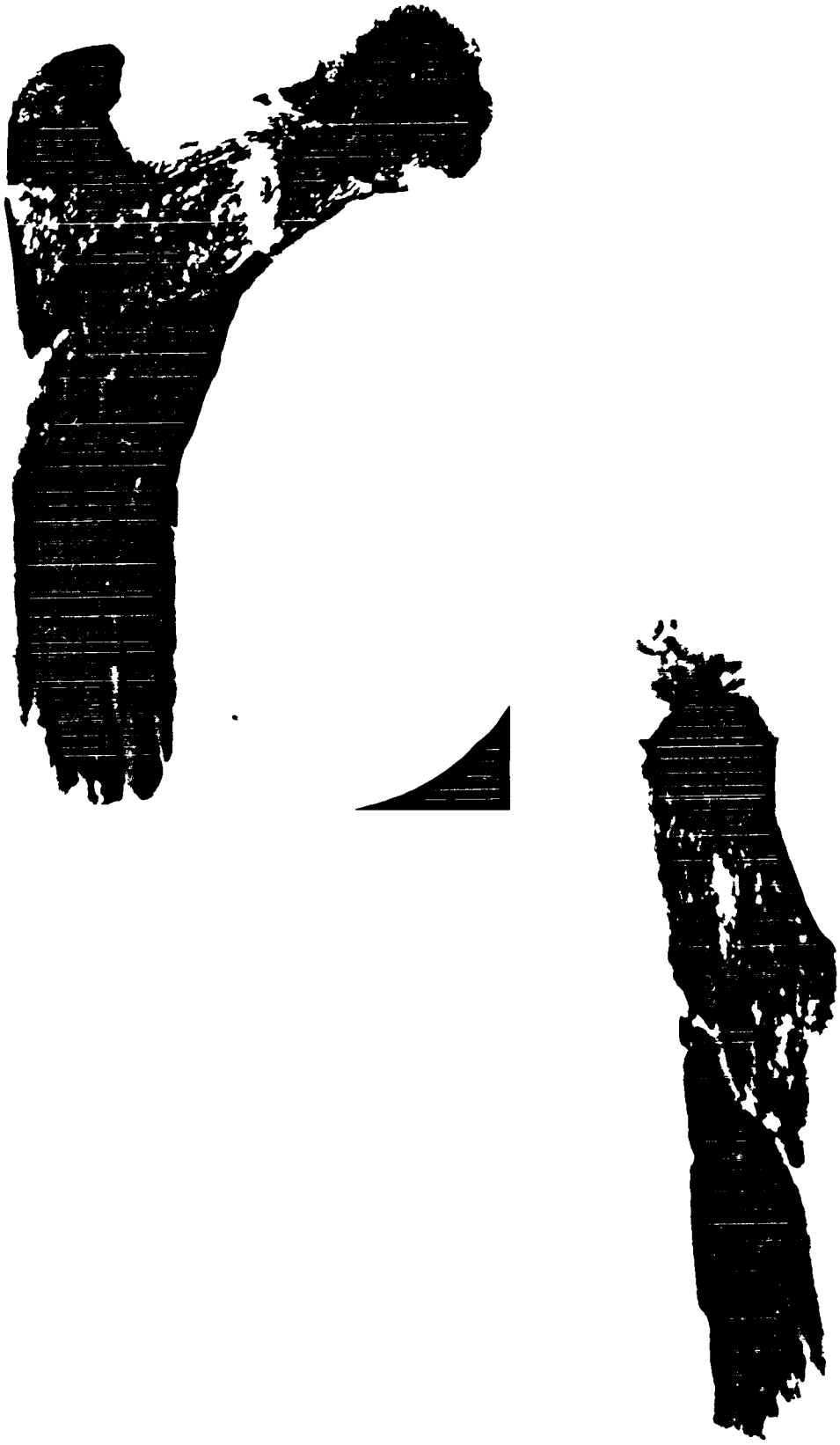
FEMUR (IV)

FEMORA I & V



PEKING FEMORA (ORIGINALS)

PLATE IV



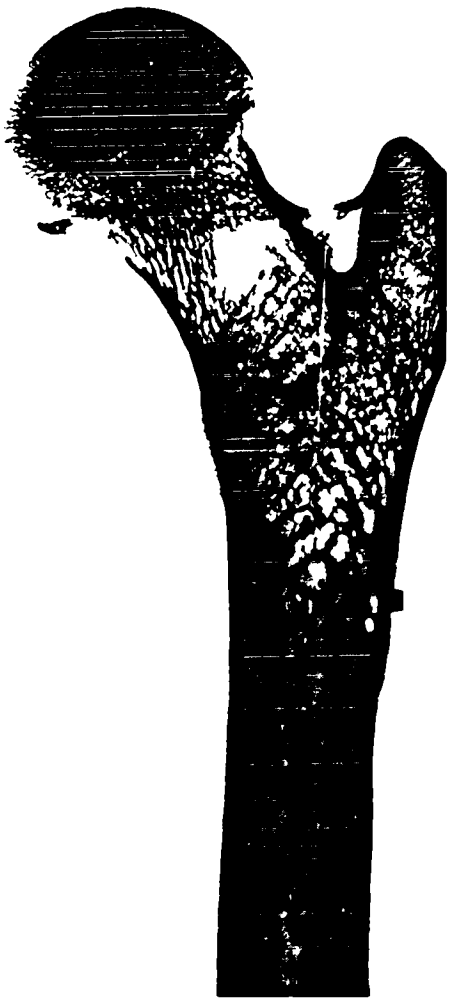
SK 82

PLATE V

SK 97

PLATE VI

ANCASTER WITHOUT
WARD'S TRIANGLE

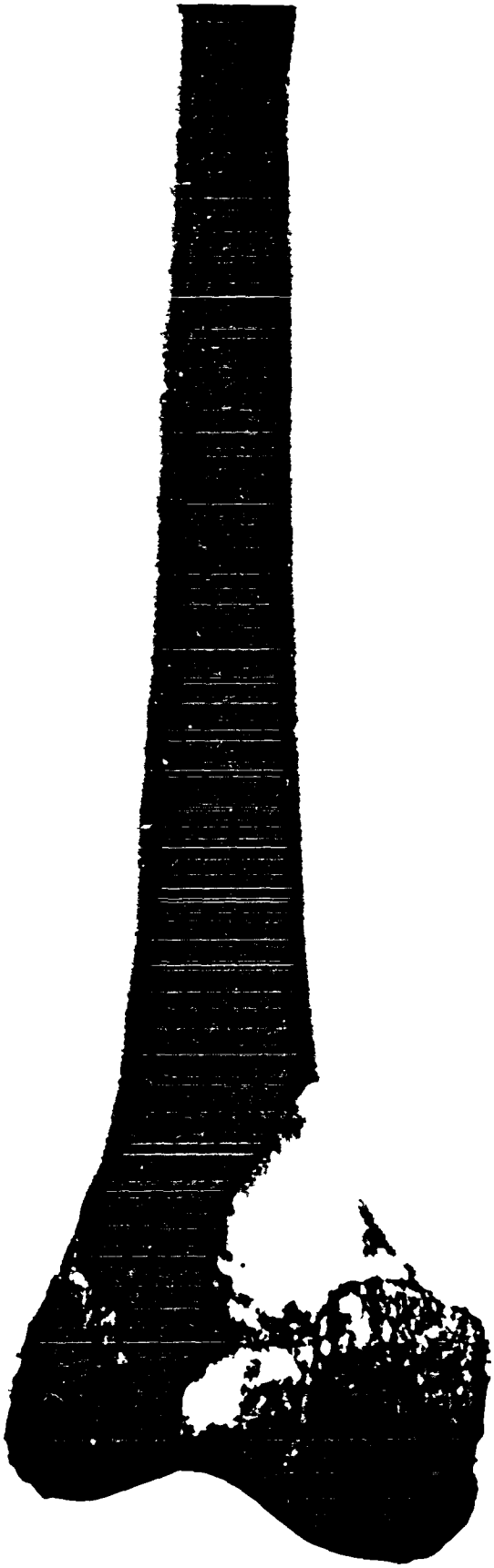


PONGO WITH
WARD'S TRIANGLE

PLATE VII A

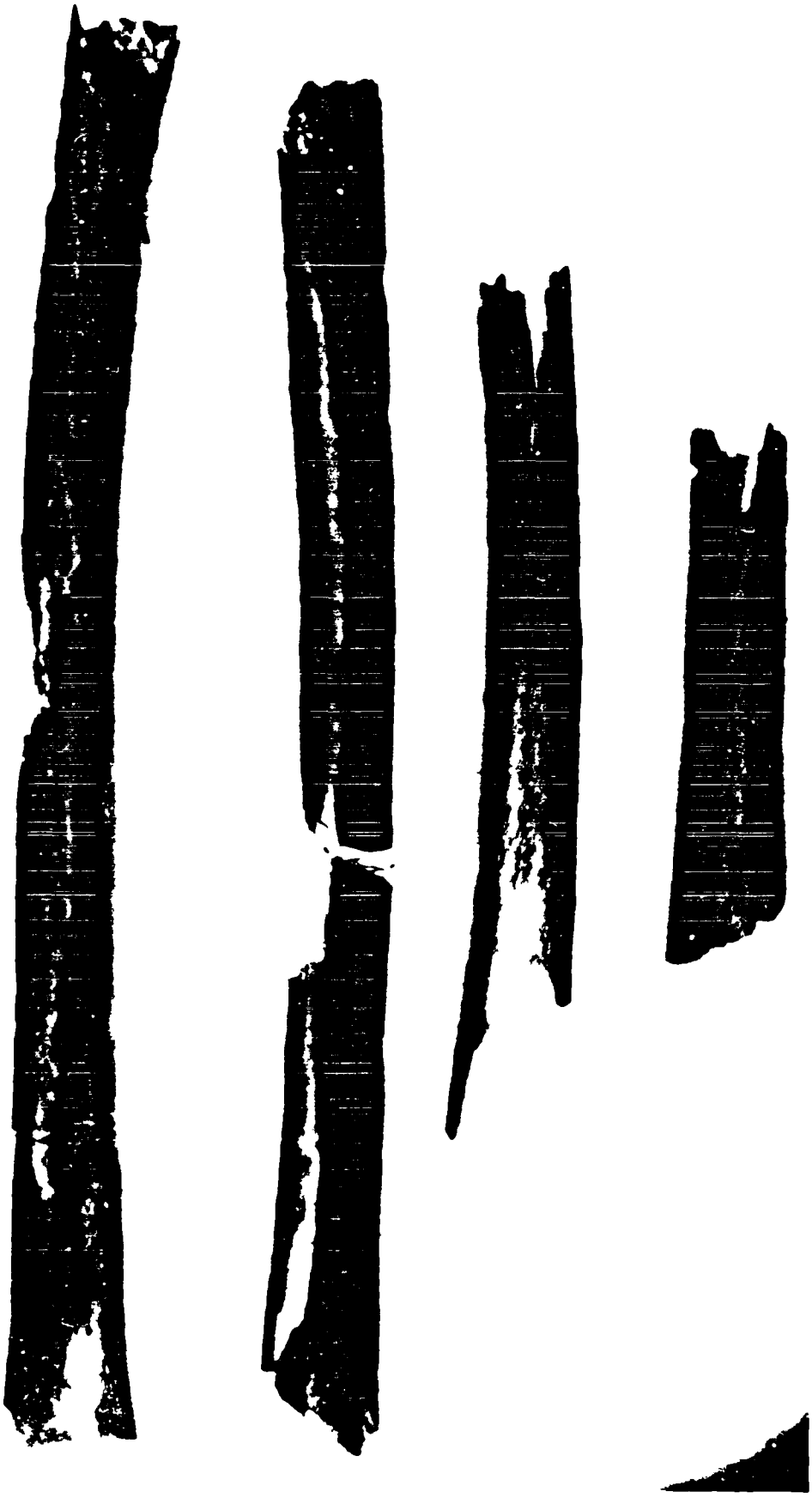
TRINIL FEMUR I

PLATE VII B



TRINIL FEMUR I

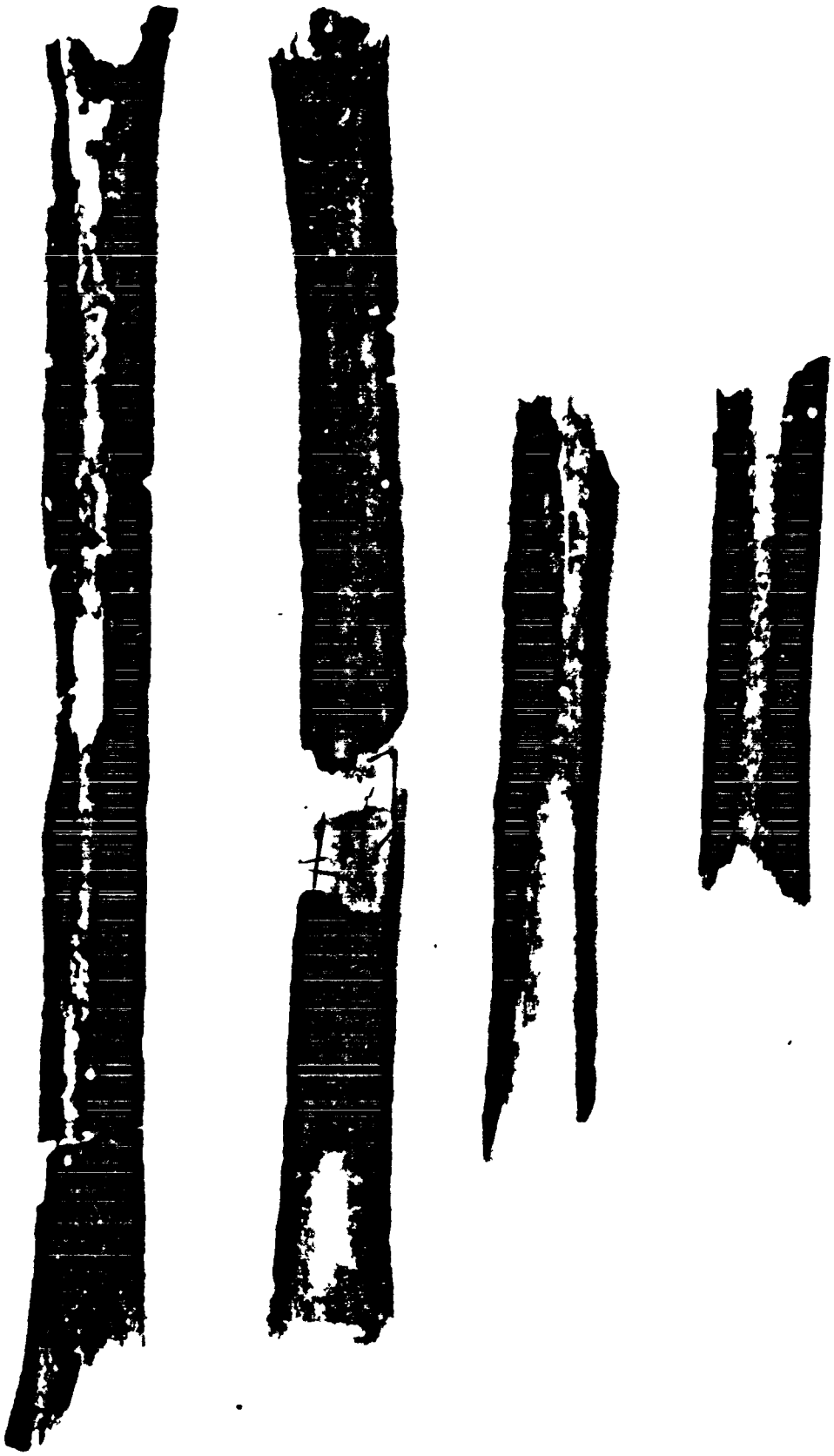
PLATE VIII



III IV V VI

TRINIL (LATERAL VIEW)

PLATE IX



III IV V VI

TRINIL (ANTEROPOSTERIOR VIEW)